THE RELATION OF PLANTS TO TIDE-LEVELS

A STUDY OF FACTORS AFFECTING THE DISTRIBUTION OF MARINE PLANTS

BY

DUNCAN S. JOHNSON AND HARLAN H. YORK

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THE RELATION OF PLANTS TO TIDE-LEVELS.

A STUDY OF FACTORS AFFECTING THE DISTRIBUTION OF MARINE PLANTS AT COLD SPRING HARBOR, LONG ISLAND, NEW YORK.

By Duncan S. Johnson and Harlan H. York.[1]

I. INITIATION OF THE WORK; ITS PURPOSE; ACKNOWLEDGMENTS.

The present studies were begun, in the summer of 1905, by Duncan S. Johnson and Mary Lentz Johnson, at the Biological Laboratory of the Brooklyn Institute of Arts and Sciences, at Cold Spring Harbor, New York. They have been continued during the summers of 1906 to 1913 by the authors.

During the progress of the work, which sometimes demanded the cooperation of several men working at once, other members of the Laboratory have aided us, among them Messrs. W. H. Brown, G. C. Fisher, W. E. Maneval, and L. H. Sharp. Thanks are due especially to Dr. C. B. Davenport, Director of the Laboratory, who afforded facilities for carrying on the work and gave suggestions concerning the construction of the maps. Professor Francis E. Daniels, of St. Johns College, Maryland, rendered valuable aid in making tide records and in surveying parts of the harbor. We have also to thank Professor H. S. Conard, of Grinnell College, Iowa, for contributing an important section of the descriptive portion of this paper. In the summer of 1909 Professor Conard, with the aid of Mr. Paul M. Collins, plotted in minute detail the distribution of the vascular plants of a carefully selected area on the Spit and one on the Marsh. The results are given in plates XIV, XXI, and XXII, and in the explanations of these on pages 113 to 121. In the summer of 1910 Miss Stella G. Streeter, of Jersey City, made a study of the rate of growth of certain Ulvaceæ, Fucaceæ, and Rhodophyceæ, of the salinity of the water in several tributaries of the harbor, and of the soil-water at several points on the Marsh. Her results are embodied in Sections III and IV. Dr. A. F. Blakeslee secured specimens of algæ for us in the winter of 1912–13. To Mr. F. S. Collins, of Malden, Massachusetts, and Dr. Albert Mann, of Washington, D. C., we are under obligation for the identification of various algæ and diatoms.

These studies have been confined chiefly to the small "Inner Harbor," on which the Biological Laboratory is located. The field work has been done by both authors in the time they could spare from their work of instruction in this Laboratory, during July and August of the years mentioned. Visits have also been made to the harbor in April, in June, in late September, and at the end of November, for the sake of comparing the condition of the vegetation at these times with that found in midsummer. This paper has been written by the senior author, except the chapters attributed to others, below their titles.

[1] Botanical contribution from The Johns Hopkins University No. 42.

The purpose of these studies has been to determine and record the distribution of the plants occurring in this harbor in relation to external conditions. The external factors considered are: topography, substratum (including subsoil), and salinity of soil-water; the time of submergence and exposure due to tides; water-currents and the effect of immersion in fresh water during low tide. An attempt has been made to determine, as far as is possible from direct observation, which of the various external factors are the effective ones in determining the distribution of each plant or plant society.

It is believed that such a record of the present distribution of the plants of this harbor, in relation to external conditions, will be of value in several ways. In the first place, the vegetation in question will serve as a type for many of the harbors on the north side of Long Island and on other parts of our coast. Secondly, the relative importance of the various factors affecting the distribution of marine plants in general may be perceived in part from a consideration of the conditions here described. Thirdly, it is also true that a comparison of the conditions and the plant distribution existing in this area two or three decades hence with those here recorded should indicate to what changes in conditions any changes in the distribution may be due. Such a comparison will certainly aid in giving a clearer conception of the causes of plant succession among littoral associations. Fourthly, in this general study of the factors affecting the distribution of these plants, the particular problems likely to yield valuable returns for experimental study have become more clearly defined. It is well understood, of course, that most of the problems of distribution here dealt with can not be adequately solved till the physical conditions of the environment are accurately measured.

II. LOCATION AND PHYSICAL FEATURES OF THE AREA STUDIED. MODE OF DETERMINING AND MAPPING THE DISTRIBUTION OF PLANTS, THE PHYSIOGRAPHY, AND TIDE-LEVELS.

1. LOCATION, CONSTRUCTION OF MAP, MODE OF DISCOVERING AND RECORDING THE POSITIONS OF PLANTS.

Cold Spring Harbor is on the north side of Long Island, 30 miles east of New York City. The Inner Harbor, with which we are concerned here, opens by a narrow channel from its northeast corner into the Outer Harbor. The two harbors are separated from each other by a spit of sand and gravel, locally known as the "Spit" or "Sand Spit," the former of which names we shall use for this barrier. The Outer Harbor opens into Long Island Sound 5 miles north of this Spit. The studies here recorded have been confined chiefly to the Inner Harbor, which, because of its size, its relatively quiet water, and its proximity to the Laboratory has proven a very satisfactory area for study.

The map of the harbor here used (plate I) has been built up from an enlargement of a map prepared in 1901 by H. R. Codwise. In the course of our work a series of contours, above and below the water-level, and many details in the topography, wharf-lines, etc., have been added to the original enlargement.

As a means of accurately locating points of importance for the topography of the harbor, or in plant distribution, several lines of range-stakes were driven in the bottom and on the shores. The main north-and-south axis in our map is along a line running due north for 2,800 feet from a large pile at the southwest corner of the Inner Harbor. This pile is about 3 feet to the shoreward of the wharf-line and 90 feet south and east of the nearest corner of the Biological Laboratory. Stakes were driven in the bottom of the harbor at intervals of 200 feet along the length of this line. Eastward from the same pile a second line of stakes, also 200 feet apart, ran over the bottom of the harbor and then across the north end of the æstuarial marsh south of the harbor. These main north-and-south and east-and-west axes were laid out by a small surveyor's compass. When tested later by a professional surveyor their directions were found to be correct within a few minutes of arc. The distance between stakes was measured with a considerable degree of accuracy, by means of a steel tape or a piece of steel wire exactly 200 feet long. This was a somewhat difficult proceeding, since nearly all the measuring on the north-and-south axis had to be done from boats. But by hooking a loop at one end of the wire over a nail in the center of the last stake set, and then placing the center of the other stake exactly at the other end of the wire, a considerable degree of accuracy was attained. The total distances measured correspond closely with those indicated by Codwise and those on the United States topographic map.

All distances mentioned in this paper, in noting the position of plant-groups or contours, are in feet, since this is the unit used in the United States topographic map and in the tide-tables published by the Coast and Geodetic

Survey. Since, however, the scale of the map (plate I) is 1:4,000, the metric value of any horizontal distance may readily be obtained by applying a metric scale directly to the map.

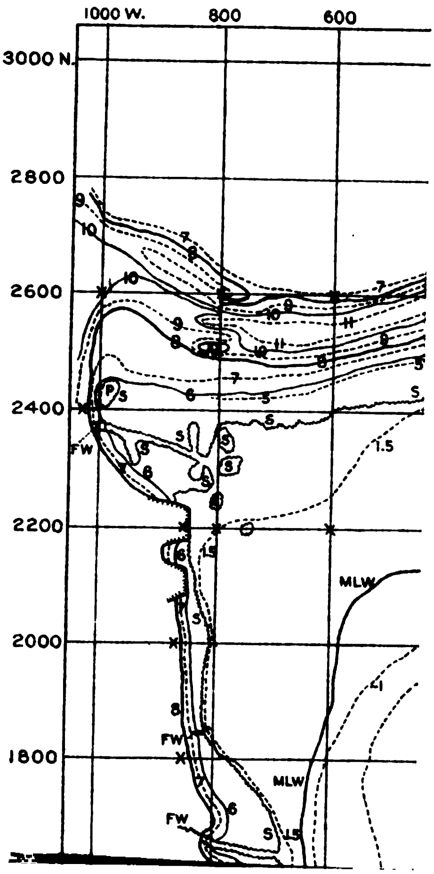
After the stakes along the two main axes were in place, stakes were set along the east and west sides of the harbor and over the Marsh and Spit to serve as range-stakes. The stakes along the sides of the harbor were set due east and west of the stakes of the north and south axis, by means of a mariner's quadrant. This is the only instrument that can be satisfactorily used in a floating boat. Stakes were placed by the aid of the same instrument, at 200 feet and 400 feet south and 200 feet north of each stake in the main east-and-west axis across the Marsh. A line of stakes at 200-foot intervals by measurement was run westward on the Sand-spit from the stake in the main north-and-south axis, at 2,600 feet north. Range-stakes were then set at 400 feet south of each of these. A similar line was run eastward from the stake at 2,800 feet north in the north-and-south axis. A range-stake was then placed 200 feet south of each of these.

When all these stakes were in place, by sighting with the aid of a field-glass one could determine the position of points in the harbor which were in range with any two stakes in the same north-and-south line, or of any two in the same east-and-west line. By measuring perpendicularly to these range-lines with a tape, the position of any point about the harbor with reference to any range-line, and so with reference to the main north-and-south and east-and-west axes, could be determined. By the intersection of the range-lines passing through the stakes of the longitudinal series with lines passing through the stakes of the transverse series, the harbor was divided off like a checker-board into squares, each square being 200 feet on a side. This is shown clearly on the map, where there is indicated by an × each intersection which was actually marked by a stake in the harbor, on the shore, the Marsh, or the Sand-spit.

The first work to be done after the harbor had been staked off was to correct in detail the outline of the harbor, with its surrounding beaches, marshes, and wharves. The heavy solid-black boundary line, shown on the map, indicates the 8-foot tide-line, wherever the harbor is bordered by the natural sloping beach or marsh. The portion of the shore-line bordered by the vertical walls of stone wharves, which vary in height from 7 to 9 feet, is indicated by the addition of short transverse lines to the heavy line of the 8-foot level. The exact outline of the shore on the east and west sides of the harbor was determined by measuring with a tape on each transverse range-line the distance of the shore-line east or west of the nearest north-and-south range-line, and so, practically, the distance east or west of the main north-and-south axis. Where the shore line is irregular measurements were made at several points between the successive east-and-west range-lines. The points so determined were plotted in on the map. With this map in hand in the field a line was drawn connecting these points and showing, as accurately as possible, the minor irregularities of the shore-line between the measured points.

The method of marking the shore-line on beach and marsh, when the water was at the 8-foot level, was the same that was used for determining and marking other tide-levels, and will be described below.

The locations of plants or the boundaries of plant groups growing on shore or on accessible parts of the harbor bottom were usually measured by rod or


1000 W.
800
600
3000 N.
2800
2600
2400
2200
2000
1800
FW
MLW

tape in the manner noted for measuring the boundary of the harbor. When the position of plants or tide-limits had to be determined in parts of the harbor where, because of water or a muddy bottom, the rod or tape could not be used, it was necessary to estimate distances within each 200-foot square. This was done by setting temporary stakes at the nearest points in the nearest north-and-south, and east-and-west range-lines, and then, after rowing away from these to the point to be located, estimating the distance in boat-lengths, and converting it into feet. The accuracy of the estimate made was considerably increased by making duplicate estimates, usually from range-lines on opposite sides of the point to be determined. The error still present in any of these estimates is small in proportion to the magnitude of the distances measured.

The procedure in determining the outlines of the areas occupied by *Zostera marina* may serve as an example of the mode of measuring distances within each 200-foot square. Starting from one end of the harbor, on a quiet day, with half tide and clear water, the boat was kept along one longitudinal range-line from end to end of the harbor. The points at which *Zostera* was first encountered (in a density of 10 or more shoots per square yard), at the south end of the harbor, and the points at which it disappeared at the north end, were noted. The distances of these from the nearest east-and-west range-line, and so from the zero-point, were then estimated. After each longitudinal range-line had been followed in this way, the boat was rowed along each transverse range-line, and the distance east or west of zero of its intersection with the boundary of the *Zostera* was noted. Connecting up the two series of points thus located tended to reduce considerably the error that might occur if the intersection of the *Zostera* boundary with one series of range-lines only had been determined.

2. TOPOGRAPHY OF THE HARBOR; ITS SIZE, DEPTH, CHARACTER OF BOTTOM AND SHORES.

The deep, narrow valley occupied by Cold Spring Harbor has been cut out from the mass of gravelly morainal deposit, which makes up this part of Long Island, chiefly by one considerable fresh-water stream. The elevation of this terminal moraine along the sides of the harbor is 50 to 225 feet above sea-level. The nearly flat bottom of that part of the valley in which the Inner Harbor lies is just covered at high water, while more than half of it is left bare at low water.

The upper, or south, end of the valley is occupied by a fresh-water stream, with a flow of something over 100 cubic feet per minute. This main stream, which we shall speak of as the "Creek," enters the harbor through a culvert under the highway, at 580 south by 820 east. A second smaller stream, largely of artesian water, coming from the pools of the New York State Fish Hatchery, enters the harbor from under the same highway, at a point 100 feet west of the main stream or Creek. A third stream, also small, is fed chiefly by springs 200 feet or so south of the highway, and it enters the harbor about 70 feet east of the creek.

Beginning at a point about 350 feet above the previously mentioned culvert, the main stream is dammed at three points to form large ponds. Each of these ponds is bordered, especially at the southern or upper end, by a densely

wooded swamp. From the lateral banks, especially the western, the ponds are fed by numerous rivulets of cold spring-water, all of them first coming to the surface within a few yards of the margin of the pond.

The Inner Harbor, as shown on the map (plate I) is, at high water, about 3,500 feet long. It has a width of about 400 feet near the south end, and widens to an extreme width of 2,200 feet at the north end. The total area of the water-surface at the 8-foot tide-level is about 5,000,000 square feet, or 110 acres. At mean low water (see plate I) the water-surface measures only 1,400 feet from north to south and 1,700 feet from east to west, the total area at this level being about 2,000,000 square feet, or 45.5 acres. At a level of 1 foot below mean low water the water-surface measures less than 700 feet from north to south, and a little more than this from east to west. At this level, however, there is a long tide-basin near the west side of the harbor, which is connected with the center of the harbor by a long tide-stream that sweeps around near the northwest corner of the harbor. The total area of water-surface when the tide is at this level is reduced to about 750,000 square feet, or 17 acres. That is, at such an extreme low tide, less than one-sixth of the bottom of the harbor is covered by water.

The deepest part of the harbor has a bottom at but 7 or 7.5 feet below mean low water, and even this depth is found only over an area little more than 100 feet in diameter. This area lies between 1,340 and 1,470 north and 500 and 610 east. The bottom of the harbor is covered over most of its area by a thick layer of fine silt, which is slightly grayish on the surface, but dense black below the upper millimeter or two. The thickness of this black mud differs in different parts of the harbor. Near the shores there may be only a few inches, or at most a foot, while near the center of the harbor (*e. g.*, at 1,800 north by 0 east) a steel sounding-rod may be pushed down 9 or 10 feet below the surface of the mud before reaching the hard gravel bottom. Since the surface of the mud at the point referred to is but little below mean low-water level, the gravel bottom is here 9 or 10 feet below mean low water.

It is worthy of note that at that part of the harbor where the water is deepest (*e. g.*, near 1,400 north by 600 east) the bottom is of sand, gravel, or shells, and is only about 7 feet below mean low water. This is evidently due to the fact that this part of the harbor is in the line of the swift current which carries on with it all but the coarsest particles. On the contrary, all the parts of the harbor bottom about this depression, except on the line joining it with the main stream and with the Inlet, *i. e.*, all parts outside the strongest current, are being filled up with the finer silt carried by the more slowly moving water. It is evident that *Zostera* plays an important part in retarding the tidal currents flowing over the harbor bottom to and from the Inlet.

The silting up of the harbor is due partly to the remains of organisms growing in it, partly to material brought down by the fresh-water streams running into it. A relatively considerable amount of material is also brought in by the flood tides from the Outer Harbor. Part of this may evidently be material carried out by the last ebb tide, but part of it may come from other streams emptying into the Outer Harbor or may be eroded from the edges of the tide channel. The filling up of the Inner Harbor is going on at a rather rapid rate. In some localities, where the presence of *Zostera* or of the very numerous

mussels slows the movement of the water, the bottom may be built up an inch, or, locally, even several inches in a year.

The only considerable areas of the harbor bottom below 1.5 feet which are at present covered by coarser materials are: the main channel of the Inlet, the deep hole at 1,400 north by 600 east, parts of the channel of the main fresh-water stream, and the bars on each side of the latter at 200 north and at 500 to 600 east. The main channel and deep hole have a bottom of gravel and bits of shell. The bars have a bottom often made up of alternate layers of mud and gravel. Because of the thinness of the gravel layers one often breaks through in attempting to walk over this part of the harbor bottom. These gravel layers are evidently spread over the constantly accumulating deposit of silt by the swifter current of the stream in times of flood. The bottom of the stream itself, from 0 to 580 south, is of gravel or small boulders in the shallow parts and of soft mud in the deeper holes. A small area with gravel bottom is found opposite the mouth of each small fresh-water rivulet along the shores of the harbor (indicated by *FW* on plate I). These are but a foot or two in width, and often reach only half-way down the beach toward low-water mark. This is probably due to the fact that the bottom from the 2-foot level downward is so extremely flat that the water spreads out over it in very small, slowly moving rivulets (plate II B); that the masses of *Ulva* present turn the water or dam it, now at one point and now at another; and that such minute channels as are cut out of the mud during the short exposure of this low-lying bottom at low tide are filled in by wash of waves and by new deposits of silt when the tide rises.

The boundary, or shore, of the harbor at the 8-foot level is in part natural, or undisturbed, and in part formed by artificial walls or wharves. The water-line of the natural shore at 8 feet is indicated on the map by a heavy solid line, usually more or less wavy, and marked frequently with a figure 8. The wharf-line is indicated by a similar heavy line, with short cross-lines added on one side. This line is generally more angular and straight, and not wavy.

Beginning on the east side, we find the harbor bordered by vertical-walled stone wharves, practically all the way from the north end at 2,800 north, down to the old mill, at 500 north and 1,000 east. Along most of this distance, *i. e.*, from 2,200 north to the mill, as indicated on plate I, the harbor bottom at the foot of the wall is at about the 1.5-foot level, while the wall extends up to a level of 8.5 or 9 feet (plate III B). South of the mill for 300 feet there is a sloping shore or beach between the 6 and 8 foot tide-levels, which is sparsely covered with gravel in some parts (plate IV B). In other parts there is between these levels a sandy or peaty soil, of from 3 to 6 inches in depth, covered with *Spartina patens, Juncus Gerardi,* and other more thinly scattered species. From about 200 north to 100 south, the water's edge, at high tide, lies at the foot of the bank of a fresh-water canal. This bank is densely overgrown with shrubs and small trees. The level of the fresh water in the canal, during the five years of this investigation, was about 25 feet above mean low water.

The 8-foot tide-line, from 160 south by 1,200 east, runs across a nearly flat æstuarial marsh, which for brevity we shall call the "Marsh." The line then runs west and northwest to 60 south by 1,000 east, then irregularly southwest, south, and westward to the road embankment at 575 south by 850 east. The western boundary of the harbor at the 8-foot level, from 625 south to 680 east, runs northward and northwestward, with a gravelly or narrow marshy shore, to

170 south by 380 east. From here northward to 20 south, then west to 0 east, and from thence northward and westward to 550 north and 230 west, the harbor is bounded by the stone walls of a tide-pool, then further on by the walls of the wharves along the south and west sides of the harbor.

The western shore of the harbor, from 550 north to 2,250 north, is a rather steep, gravelly beach. The only exceptions to this are the stone wharf, with wooden piles, from 1,070 north to 1,220 north, a stone wall from 1,410 north to 1,560 north, and two stone and wooden wharves from 2,080 north to 2,250 north. From 2,250 north this shore is muddy and is covered rather completely with *Spartina glabra alterniflora* up to the extreme northwest corner of the harbor near 2,600 north by 1,000 west.

The Spit, which is 100 to 175 feet in width, and has an elevation of from 10 to 12 feet above mean low water, forms the northern boundary of the harbor. The south beach of this Spit, between the 6.5 and 8 foot tide-lines, differs in character in different parts of its extent. From 1,000 west to 700 west the shore is of sandy loam, very flat, and covered with a dense growth, made up almost entirely of *Spartina patens* and *Distichlis spicata*. From 700 west to about 300 east, the beach is steeper and often nearly bare for considerable stretches (plate IV A). Where covered at all it is usually by small patches of *Spartina patens, Suæda*, or *Salicornia*. From 300 east to 900 east, the similar gravelly beach is covered, often completely up to 7.5 feet, by a dense growth of *Spartina, Distichlis, Suæda*, or *Salicornia*. Any one of these may occur locally in a pure stand, or, in other places, all may be more or less mixed together. Among these seed plants, on the bases of their stems, or on the gravel and sand of the otherwise bare portions of the beach, dense mats of incrusting algæ of many species occur in patches a yard wide and several yards long, giving the beach a dark greenish or black color. These types of vegetation will be described in detail later.

The extreme eastern end of the Spit, beyond 825 east, is entirely bare between the 7-foot and the 8-foot levels, being essentially similar, except for the finer sand of which it is made up, to the wave-beaten outer side of the Spit at this same level.

3. TIDE-LEVELS; MODE OF DETERMINING HEIGHT AND RATE OF RISE AND FALL OF TIDES.

One of the primary facts we wished to determine concerning the habitat of each species of plant growing in our area was the position of this habitat with reference to the tide-limits. Thus only could we determine how long, in each 24 hours, the particular habitat is submerged and how long exposed to air, sun, and rain. Our aim was to discover just how definitely the distribution of beach and marsh plants is dependent upon the relative times of submergence and exposure of the plant-shoot and of the substratum upon which it is growing.

The first step in accurately determining the relative times of submergence and exposure of any particular zone of beach or bottom is to establish a standard datum-level from which to measure the height of tides. This was done by placing a graduated tide-stake near the middle of the harbor, with its zero-point at mean low water. This stake was planted on a very quiet day, when, according to the Tide Tables of the Coast and Geodetic Survey, the

lowest stage of the tide was expected to reach exactly to mean low water. The correctness of this standard was checked later by other observations of the tide-level at both low and high water, and also, on quiet days, by comparing the level recorded on our stake with that predicted by the Tide Tables. This stake was graduated to feet and tenths of a foot for 2 feet below and 9 feet above the zero-point.

When this standard tide-stake was once established, other similar graduated stakes were placed by the wharves on the east and west sides of the harbor, where records of the rise and fall of the water could be more readily made.[a] Stakes were also placed near the dense growths of algæ and other plants whose distribution was to be studied. A permanent reference level or benchmark was cut into a stone on the northeast corner of the foundation of the Biological Laboratory, at 14 feet above mean low water. Records of rise and fall of the tides were made by noting the time the water reached each foot and half-foot mark on the tide-stake. Just before and after low water and high water the record was made for each tenth of a foot. This gives a more satisfactory record than that obtained by noting the height of the water at each interval of 10 or 15 minutes, since the contour-lines between tide-marks on the beach and marsh were determined for each half-foot interval. The records of the rise and fall of tide at the standard tide-stake were usually begun at or just before low water, and were continued through the rise to high water and through the succeeding fall to the next low water. In some cases the record was continued for 22 or 24 hours, in order to get the daily variations or differences in the height of low water and of high water in the two successive tides of each day.

In the tide-curves here given, distances along the vertical axis indicate the height of the water above mean low water, in tenths of a foot, except at the middle and straighter part of the curve. Horizontal distances indicate time in intervals of tenths of an hour. The curve published in plate VI shows a rather slowly ascending rise, taking nearly 2 hours, from low water at −0.2 foot to +1 foot; a steep, nearly straight curve, taking 2.5 or 3 hours, from 1 foot up to 6 feet; a very slow and irregular rise, taking about 2 hours, from 6 feet to 7 or 7.5 feet. On the descent there is a slow and somewhat irregular fall from 7 to 6 feet or from 7.5 to 6.5 feet, lasting about an hour and a half; then follows a rapid descent to 2 feet, taking but 3 hours, and finally a slower fall from 2 feet to 0.2 foot in the morning tide or to 0.5 foot in the afternoon tide. This fall of 1.5 or 2.2 feet takes 2.5 hours, or nearly as long as is required for the drop of the 4 or 4.5 feet next above. The flattening of the curve on this side of low water is even more marked than that shown on the rise.

In a confined harbor with a narrow inlet and with a surface area that may change very considerably with a slight change in level, it is to be expected that the tide-curve will show marked irregularities. As a matter of fact, the whole rise up to 6.5 feet gives a very regular curve. As one watches the rise of the water, however, between 6 and 7.5 or 8 feet, he sees the water remain almost constant at one level for many seconds or even two or more minutes, and then, suddenly, in a minute or less, go up a tenth of a foot. The record for the night tide, given in the curve on plate VI, shows this sort of irregularity very

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[a] See footnote on p. 133.

clearly, between 7 and 7.5 feet, in both rise and fall. This record was taken on a night when the water was so quiet as to insure accuracy, and the irregularities referred to are thus not at all due to waves or other local irregularities in level.

An examination of the map shows that the 1.5-foot contour is widely separated horizontally from the zero or mean low-water contour. That is, the area of the harbor bottom to be covered increases with great rapidity as the water rises from 0 to 1.5 or 2 feet. This seems evidently part of the explanation of the slow rise shown by the start of the curve in plate VI. On the other hand, the horizontal distance between the 2 and 6-foot contours is relatively small, which is probably related to the steepness of the curve between 2 and 6 feet. While the 6 and 8-foot contours are close together about much of the harbor, they are widely separated on the Marsh at the head of the harbor. This probably is a partial explanation of the flattening of the top of the tide-curve. It must be kept in mind, however, that the form of the tide-curve in the Outer Harbor, or the varying cross-section of the Inlet, may be concerned in determining the form of the curve for the Inner Harbor. In fact, published curves for the tides of more open water show that there is often a flat crest and trough, even at the open shore of the ocean. (See Darwin 1910.)

The matter of primary importance for us is the actual form of the curve for this particular harbor, without regard to the ultimate causes of this form. It will become evident, however, that those factors that determine the time at which the water reaches and leaves a given level on the beach give the time of submergence and exposure and determine, in part at least, which plants shall grow at that level.

One can easily determine the time of submergence or exposure of any given level along the beach or wharf by consulting the tide-curves. This can also be calculated by subtracting the time of submergence from the time between one low water and the next following low water. The latter time varies from less than 12 hours, in the case of spring tides, to 13 hours, in the case of neap tides, the average interval being not far from 12.5 hours. Table A (p. 135) gives the average time of submergence and exposure for various levels from 0 to 8 feet. This will be useful for reference when we come to describe the distribution of the plants of the harbor.

A comparison of curves or records for neap and spring tides shows that the time of daily submergence of levels below 2 feet and that of emergence of levels above 6 feet is decidedly greater during neap tides than during spring tides. On the other hand, for levels between 2 feet and 6 feet the time of submergence, like the emergence, is practically the same for both kinds of tide. This latter fact is clearly indicated by the straightness of both sides of the tide-curve between the levels mentioned. This means, of course, that plants growing in this zone of about 4 feet in vertical width have a practically constant proportion of daily submergence and exposure, from end to end of the growing season. On the beaches it is just this zone that is dominated by *Spartina glabra alterniflora* (plate VII A).

The plants of the harbor bottom below the 2-foot level and those of the beach above the 6-foot level are subject to much greater variation in the proportion of daily submergence and exposure. It might be assumed that this variation within each fortnightly period, *i. e.*, within each set of tides, is

of no importance, and that the total times of submergence and exposure each fortnight, or for the whole growing season, are the decisive factors limiting the distribution of a plant. There is, however, good evidence that the long exposure during an extreme low tide on a clear, hot day may result fatally to plants that have flourished during average tides, *e. g., Ulva* seems often to be killed off by long exposure and drying up, after the draining off of the water from the underlying mud.

TIDE-LINES.

After the standard tide-stake and the accessory stakes were established, the method of determining the position of the 5, 6, 7, and 8 foot contours, or tide-lines, on the beach was as follows:

An observer stationed near a tide-stake gave signals by a whistle or flag when the water had risen to within 1 inch of the level to be marked, another signal when the water reached the exact level, and a third when it reached 1 inch above this. One or more workers on the beach, with bundles of stakes, each marked with the height of the level that was being determined, began to set these at 50-foot intervals along the beach. On hearing the first whistle, stakes were set at an estimated height of 1 inch vertically above the water-line. At the second signal the stakes were set exactly at the water's edge. At the time of the third signal they were set in water 1 inch deep. By knowing the rate of the rise of water at that stage of the tide, the stakes could be set nearer and nearer the water's edge after the first signal, and deeper and deeper in the water as the third signal approached. Thus the exact position of the water-line was marked quite accurately by stakes for each foot from the 5-foot level to the 8-foot level. The position of each stake was then plotted on the map, and with map in hand in the field these points were connected up to form the contour-lines.

The contours of the Marsh and Sand-spit, above 8 feet, were determined by a surveyor's level. The —1-foot, 0-foot, +1-foot and +1.5-foot contours were plotted by noting, when the water was at each of these levels, the point of intersection of the water-line with each of the longitudinal and transverse range-lines. The contours between —2 feet and —7 feet were determined by soundings.

The stakes marking the 6-foot, 7-foot, and 8-foot tide-lines were left on the beach throughout the season. By the aid of these it was possible accurately to determine the exact vertical distribution of the plants of beach and Marsh. The vertical distribution of plants on each wharf was determined by the graduated tide-stake beside it.

III. PLANT ASSOCIATIONS; CHARACTERIZATION OF THE BELTS OR ZONES OF VEGETATION AND THEIR DISTRIBUTION.

We will begin our discussion of the vegetation with a descriptive account of the plant associations found in the harbor, noting their composition and distribution. Then will follow a general discussion of the factors determining distribution, and a list of all plants found, showing the distribution of each species and the relation of each to the factors affecting its distribution.

In defining the limits of the zones of vegetation in this harbor we shall use the term "littoral" in a more definite way than we have found it used by other writers on the distribution of marine plants (see Lorenz, 1863; Kjellman, 1877; and Warming, 1906). We shall designate as littoral the zone extending from mean low water up to mean high water, which, for our harbor, is a zone 8 feet, or more exactly of 7.8 feet in vertical width. The littoral zone of this harbor is distinguished, in a manner determined by the vegetation itself, into lower littoral, mid-littoral, and upper littoral subzones. The region just below mean low-water level, of which 1.5 feet may be exposed at extremely low tides, will be referred to as the sublittoral zone. The zone of 3 or 4 feet above mean high water, which may be flooded by occasional high tides or storm tides, will be called the supralittoral zone.

The most clearly marked primary vegetational groups or plant associations in the harbor are these:

(1) Plankton, made up of the plants floating at the surface in a living condition, chiefly diatoms and Peridineæ.

(2) Plants at the bottom of the harbor, between the —5-foot and the +1.5-foot levels. These occupy the soft, muddy, sandy, or pebbly bottom, or are epiphytic upon plants which grow on this bottom. The shifting pebbly or shelly bottom in the deepest part of the harbor is bare of fixed vegetation up to the —5-foot level mentioned, which thus marks the lower boundary of the belt under discussion. The upper limit of this belt is at the +1.5-foot level, where the soft mud, forming most of the bottom, is succeeded by a soil that is rendered firm by the close network of rhizomes and roots of *Spartina glabra,* which occupies the next succeeding belt on shore. This lower limit of *S. glabra,* with its sudden change in elevation of the bottom, in character of soil, and in the vegetation covering it, forms a very prominent topographic boundary. It is therefore indicated on our topographic map.

(3) The mid-littoral belt of vegetation occupies the shore between the 1.5-foot and 6.5-foot levels. On muddy shores a fringing marsh of *Spartina glabra* dominates between these levels to the exclusion of all other seed plants, save a few small groups of the inconspicuous umbellifer *Lilæopsis lineata.* Numerous algæ, however, are found on the mud between the stalks of the *Spartina.* Many of them are species not found elsewhere, and most of them are associated in mats or felts of a sort not occurring in other locations except in the next

A. Looking over Harbor Bottom at Low Water, from 200 North × 600 East toward 2,600 North×400 West, showing *Ulva* covering Bottom, and Tide Channels from Creek.

B. Looking over Harbor Bottom from 100 North × 40 West to 600 North × 1,000 East, showing *Ulva* on Bottom and Tide Channels from Tide Pond; at Right Middle Ground the Northernmost Tongue of *Spartina glabra alterniflora* from Marsh.

higher belt, where these associations have a somewhat different make-up. On stony substrata within the limits of this belt, which are confined practically to the walls of the wharves, we find a nearly continuous rockweed association. This is dominated by *Fucus vesiculosus, F. evanescens,* and *Ascophyllum nodosum,* but it embraces also a considerable number of smaller algæ of all classes, many of them very numerous. A few of the latter are found on the fringing marsh also, but most of them are not.

(4) The upper littoral belt extends from 6.5 feet to 8 feet. On gravelly, well-drained portions of the shore this level is usually dominated by *Salicornia* or *Suæda,* and less frequently by *Spartina patens,* often mixed with *Distichlis.* These are the areas that we have called "upper littoral beach." On flat, poorly-drained shore with peat-like soil we find an upper littoral marsh dominated by *Spartina patens,* by *Distichlis spicata,* or by *Juncus Gerardi.* Where the soil is more or less saturated with fresh water *Scirpus americanus* dominates. This apparently corresponds in most respects to the "salt-meadow" of Warming.

(5) The supra-littoral belt of vegetation extends from high-water level at 8 feet upward as far as the direct influence of the sea is felt by the vegetation, which is often 10 feet and on the Spit up to 12 feet. In this belt also we find two distinct associations, determined by the character of the soil, especially by its drainage. In sandy, well-drained portions, which are found only on the Spit, we find a supra-littoral beach, or storm beach, dominated by *Ammophila arenaria,* with which are associated three or four prominent species of dicotyledons and a score of other species, chiefly seed plants, of less frequent occurrence. On flat, undrained portions of the shore between these levels, where the peaty soil is subjected to submergence by spring tides, and is in many places kept continually moist by subterranean fresh water, we have a supra-littoral marsh, the "higher littoral marsh" of Warming. This sort of marsh is well-developed only at the head of the harbor. Near the 8-foot level the soil-water is brackish or nearly salt, while near the upper limit of this marsh at the 9-foot level the soil-water is practically fresh, at least during the growing-season. In consequence, evidently, of this difference in salinity, and in other soil characters, as well as in elevation, the vegetation differs greatly in different parts of the marsh. The lower, more saline portions are dominated by *Spartina patens* or by *Juncus Gerardi,* while fresher areas are characterized by *Scirpus americanus,* and the highest parts are occupied chiefly by *Aspidium thelypteris.*

1. THE PLANKTON.

The plant constituents of the plankton of the Inner Harbor consist of a relatively few species of diatoms of the genera *Melosira* and *Navicula,* and a few species of Peridinaceæ. Of the latter one species of *Glenodinium* often occurs in such numbers, over areas of scores of square meters, and to a depth of 0.5 meter or more, as to color the water a deep brown. This condition was frequently noted two or three times a summer, and often lasted for several successive days. Professor C. B. Davenport informs us that this or a similar species of the Peridineæ is sometimes so abundant in September as to kill many of the fish in the harbor by clogging their gills. The time at our disposal did not suffice for a detailed study of the plankton and its daily and seasonal variation.

2. THE BOTTOM VEGETATION OF THE HARBOR FROM -5 TO +1.5 FEET (THE SUB LITTORAL AND LOWER LITTORAL BELTS).

The present belt includes 1.5 feet of the lower part of what Kjellman calls the "littoral region," *i. e.*, of the strip between low and high tide marks. It also includes 5 feet vertically of bottom below the mean low-water level, *i. e.*, 5 feet of what Lorenz calls the "submerged littoral region."

The plants forming the bottom vegetation of this harbor consist of (A) plants of the loose soil; (B) algæ attached to stones or shells; (C) epiphytes living chiefly on members of group A.

A. PLANTS ON LOOSE SOIL (THE ENHALID FORMATION OF WARMING).

This formation includes two seed plants, *Zostera* and *Ruppia,* which are rooted in the soft bottom, and only two important algæ, *Ulva lactuca* and *Enteromorpha clathrata.* Most of these latter are unattached, and either simply rest on the bottom or are weighted down by mud or mussels. The *Ulva* grows in sheets, the *Enteromorpha* in tangles. In looking down on the bottom of the harbor from the neighboring hills at low tide, *i. e.,* with the water-surface at —1 foot, the bottom over most of its area appears green in color. This green color is due to the presence of the more or less uniform covering either of *Ulva lactuca* or of *Zostera marina,* or, on some smaller areas, of *Enteromorpha clathrata.* The most considerable bare area on the part of the bottom, exposed by the lowest tides, is that at the north and northwest portions of the harbor, which lies between the —1-foot level and the 2-foot level. Besides this there are two or three narrow strips, 12 to 15 feet wide, and trending more or less northward from the mouth of the main fresh-water stream at 200 north by 550 east, which are rather constantly bare. (See plates II and VIII.) There are other smaller changeable bare spots on various parts of the bottom outside the *Zostera* belt.

Of those portions of the harbor bottom still covered when the water is at —1 foot, the bottom of the tide-channel starting near the wharf of the Research Laboratory at 1,100 north by 400 west, and emptying into the deep hole at 1,400 north by 400 east, is nearly bare of *Ulva* and *Zostera.* Likewise, the greater portion of the deep hole itself, and of the channel leading from it to the Outer Harbor, have a rather bare, sandy, shelly, or pebbly bottom, except for that portion to the east and south of the deep spot which is indicated on the map as covered with *Zostera.* The plants of *Ulva* found under these more swiftly moving waters are small attached plants which are evidently being carried along with their supports. The area occupied by a dense growth of *Zostera* is indicated on the map by a wavy outline marked *Z.* Its distribution will later be described in some detail.

The rest of the harbor bottom below the 1.5-foot level, aside from the bare areas mentioned above, is rather completely covered with *Ulva.* This *Ulva* occurs in the form of innumerable detached flattish, or crumpled, or bullate and often perforate and ragged sheets, of all sizes from a few decimeters to 10 meters across. The distribution of much of this *Ulva* over the bottom is more or less inconstant. Often the bottom is covered completely for hundreds of square meters, *e. g.,* 400 to 1,000 north by 200 west to 400 east. In other portions of the harbor only one-half or three-fourths of the bottom is actually hidden by the *Ulva, e. g.,* near the west side at 0 to 600 north, or near 200 north by 400 west.

On closer examination of the *Ulva* plants of the harbor, it is found that practically the only attached plants present are relatively small, being 1 to 5 or 6 dm. across. These are found chiefly on pebbles and shells along the sides of the channel of the Inlet leading to the Outer Harbor and beside the main fresh-water streams, *e. g.,* at 200 north by 550 east, at 200 north by 950 east, at 2,380 north by 980 west. A few attached plants were found on stakes, on buoys, and on shells of living mussels in various parts of the harbor. A very few attached plants occur on the rhizomes of *Spartina glabra* and on stones of the wharves in the next higher belt. The widespread, though sparse, distribution of these plants in the harbor probably indicates that zoospores are abundant there. The practical absence of attached plants from most parts of the harbor bottom is evidently due to the lack of proper substrata, except where entering streams or tidal currents leave a surface of coarse particles on the bottom. The detached sheets of *Ulva* covering the bottom may become secondarily fixed by the attachment to them of numerous mussels or of snails. In other cases parts of the sheet of *Ulva* may be buried, and thus fixed, by the mud shifted by water-currents or by burrowing animals.

The general distribution of *Ulva* described above is that found each summer, in July and August, for six years past. The exact size and position of the minor bare spots in the *Ulva* zone changes from year to year, and in fact from week to week or even from day to day, due to the movement of the free *Ulva* by water-currents. In December 1912 the *Ulva* was about as abundant in the harbor as in summer. The bottom of the harbor was reported as nearly bare of *Ulva* in February 1913. In the following April, however, Dr. A. F. Blakeslee found many small sheets on the mud at the south end of the harbor.

A somewhat detailed examination of the harbor in April 1911 showed that the bottom above mean low water is much less completely covered with detached *Ulva* than in midsummer. In fact, large sheets were almost wanting in those parts of the harbor that could be examined. On the other hand, a search for attached *Ulva,* in the places where it occurs in summer, showed that it was far more abundant in April. On the east side of the channel to the Outer Harbor, for example, there were thousands of attached plants of *Ulva,* of all sizes up to 1.5 or rarely 2 dm. across, and all of them were evidently growing vigorously. In July 1911 these same areas bore a much smaller number of plants, of which the largest in the middle of the channel were about 6 or 8 dm. long. In the inrushing tide near the Inlet one may always find plants of *Ulva* or parts of plants floating in with the current, and thus being carried to the quiet parts of the Inner Harbor, many of them settling on the bottom with the next fall of the tide. These floating sheets are evidently plants that have been broken off from their supports or substrata in the Inlet and elsewhere where young plants are developed abundantly. The maximum size of fixed plants found in the Inlet in July 1911 (about 6 dm.), is probably the size at which the tensile strength of the base of the plant is just able to withstand the strain of the swiftest tidal currents. Plants larger than this are torn off, or carried away with their supports, as even smaller ones also may be, and are thus added to the covering of the bottom of the Inner Harbor.

It seems clear from the facts just mentioned that the large, free sheets of *Ulva* in the Inner Harbor are developed by the continued growth and crumpling of the relatively small and flat plants that have been torn from their

original attachment in the Inlet and on other pebbly bottoms of the harbor. Such detached plants of *Ulva* do not necessarily lodge within the *Ulva* zone the first time that they are washed into the harbor; neither do they stay indefinitely at the point where they first lodge. Even larger sheets that have been resting on the bottom for days or weeks may be moved about by the water in one of two ways. In the first place, sheets that lie on the flats bordering the tide-channels may be rolled up by the tidal current of large, swiftly flowing spring tides, and gather additional sheets as they are tumbled along over the flats, until rolls are formed 0.5 meter in diameter and 2 or 3 meters long. These rolls have been seen to roll for 40 or 50 meters over the shoals near 2,000 north by 200 to 800 east. Such rolls may evidently either be carried out to the Outer Harbor, or be broken up again, with considerable tearing of the sheets, and the fragments floated back to be redistributed over the bottom of the harbor. The long bare strips of bottom noted above are often merely the trails of such rolls.

The second mode of transportation is one that is seen on days that are bright and windy, during extreme low water, especially of spring tides. The long exposure of the *Ulva*-covered parts of the bottom at such times allows the water to drain off and permits air, and probably other gases from the underlying mud, to collect under the coarsely crumpled sheets. With the rising of the tide these sheets or portions of sheets of *Ulva* are floated up 2 or 3 feet off the bottom or even to the surface at high water, and finally, becoming entirely free from the bottom, they are blown by the wind along the surface of the water. Such floating plants may drift about the harbor and then out through the Inlet with the next fall of the tide, or they may settle in new places on the bottom, or with stronger winds they are sometimes blown to the shore, where they may become tangled among the reed grass or drifted on the beach. Windrows of *Ulva* thus formed are often found on the beaches between the 3 and 8 foot levels, or caught in the *Spartina glabra,* sometimes covering many square meters. There the plants finally die from exposure to the sun and rain. Just what part this floating of the *Ulva* may play in finally denuding the bottom of the harbor was not determined by an actual counting of the floating sheets and a measurement of their sizes, but it is evident that it may be a very considerable one. It is, however, probably small in comparison with the destruction and transportation of *Ulva* accomplished by the ice, though the importance of this factor is also undetermined, since we have not been able to study the harbor in detail in winter.

If the history of the sheets of free *Ulva* found on the harbor bottom in July is that which has just been suggested, then it is certain that the growth of those plants which settle in favorable places must be very rapid. One of the larger sheets measured in August was found to be 10 meters long and about equally broad. The production of such a plant as this in 3 or 4 months from one 6 or 8 inches across indicates the remarkable average rate of radial growth at all parts of the margin to be 30 or 40 mm. per day.

Assuming that the largest plant seen in July 1911, located just aside from the swiftest current, had come from the largest plants seen in April 1911, the rate of growth would average only 8 or 10 mm. per day. Actual measurements by Miss Stella G. Streeter of the rate of growth of somewhat smaller plants growing under natural conditions in July and August 1910 give a daily incre-

ment much smaller than this. For example, a series of young plants averaging 26 mm. in length increased to an average length of 55 mm. in 20 days. The average daily rate of growth was 1.5 mm. and the maximum daily increment was 2 mm.

It is of course possible that the large sheets of *Ulva* may winter over in some of the deeper, more protected parts of the Inner Harbor, and less probable that they may be washed in from the Outer Harbor. The rates of growth actually observed indicate that the largest of these plants can not be produced from spores in a single season. It is hoped that observations now under way may definitely determine the age of these larger sheets. It is of course possible that the larger amount of sewage present in the water in summer, during the session of the Biological Laboratory, may enable the *Ulva* to grow more rapidly than in winter or spring. (See Cotton, 1911, and Letts and Richards, 1911.)

The lower limit of distribution of attached plants of *Ulva* in the Inner Harbor is very near the mean low-water level. Plants which are drifting with their supports and torn off bits may be found at greater depths, but we have not determined how long they can persist there, and there is no adequate evidence that zoospores of *Ulva* develop to young plants at levels more than 6 inches below mean low water. Why this species is confined to levels which are exposed to air and light has not been determined, but apparently it is due to the direct effect of some physical factor, since there are, in most places, no competitors, and there are, at least in some places, suitable substrata for attachment some distance below this limit.

Since *Ulva* occurs in the next higher zone, we may discuss the factors determining its upper limit in that connection.

Ulva probably influences the distribution of other plants only as it forms the substratum for certain epiphytic diatoms and a few species of blue-green algæ, of which latter *Spirulina* is the only form of any importance. It is probable also that the smooth sheets of *Ulva* lying on the mud may prevent young seedlings and broken off bits of *Zostera* from getting a hold in the mud. Finally, the floating masses of *Ulva,* like other flood trash, may smother out many square yards of *Spartina patens,* or other plants already established on the marshes, by settling on them with the fall of the tide. The bare patches so formed often become re-covered first with *Vaucheria* or seedling *Salicornias,* as will be described later.

Enteromorpha clathrata: This plant, as we shall find, is not by any means confined within the 1.5-foot contour line, but may be found as high as the 6 or 6.5-foot level. It does, however, occur far more abundantly on the bottom of the harbor than elsewhere. As one rows over the harbor just before low water on a quiet day, he will see on the leaves of *Zostera* numerous tufts of sparsely branched, crinkled, green, tubular filaments, 1 or 2 mm. in diameter, and commonly from 5 to 20 cm. in length. These are the young plants of probably a few weeks growth of *Enteromorpha clathrata.* Observations made in the Outer Harbor show that this species may grow from the zoospore to a length of 4 inches in as many weeks. After these plants have grown to 8 or 10 inches many of them, like the young plants of *Ulva,* are broken away from their supports and float about in the harbor, to finally grow into the great tangles that settle down on the *Ulva* and *Zostera,* sometimes covering dozens or scores

of square yards of the bottom. In the more quiet areas the *Enteromorpha* may form tangles of considerable size while remaining attached to the *Zostera* on which it germinated. The later history of these tangles of *Enteromorpha* is similar to that of the sheets of *Ulva*. They are often floated up by gases accumulated in the cavity of the tubular thread. They then drift about the harbor, to lodge on some new part of the bottom and continue active growth, or they may settle on the beach or on top of *Spartina glabra*. On the south shore of the Spit masses of *E. clathrata* with some intermingled *Ulva* may crush down 75 or 100 square yards of *Spartina,* in some cases smothering out the rhizomes also and leaving a bare strip. Such tangles as lodge on the beach or on the salt reed-grass die and then break up and wash away or settle down to form part of the soil among *Spartina* stalks. Smaller bits of the living alga may settle on the mud between the *Spartina* stalks, or among pebbles on the beach above the *Spartina,* and there take part in the formation of the composite mats or felts of which other green or blue-green algæ form the major part. Of its distribution there we shall have something to say when discussing the other algæ of these higher levels. Despite the fact that it floats more readily because of the gases within its filaments, the freedom of movement of *Enteromorpha* is on the whole less than that of *Ulva*. Because of its filamentous form *Enteromorpha* becomes more readily entangled with other objects on the bottom, and it is also more often weighted down by young mussels which become attached to it in thousands. On the bottom from the 6-inch to the 1.5-foot levels, where *Zostera* and mussels are usually wanting, the tangles of *Enteromorpha* are also rare. The usual absence of *Enteromorpha* lower than about 3 feet below mean low water seems also determined by the absence below this level of organisms such as *Zostera* and mussels, with which it may become entangled or weighted down. It is true that small mats of this alga are sometimes seen below the limit of the *Zostera* in the deep hole at 1,400 north, but these are apparently all in transit to or from the Inlet. Younger plants attached to stones are found all along the Inlet from 3 feet downward, some being found even in the deep hole. These plants must form an additional though relatively unimportant supply of free plants which may grow into tangles like the more numerous plants starting on the *Zostera.*

Zostera marina: This "eel-grass," because of its abundance, gives character to large areas of the harbor bottom at low tide, and also forms an important substratum on which grow several species of epiphytic algæ. For this reason the region covered by a dense growth of *Zostera* has been indicated by a wavy outline on the map showing the topography of the harbor (plates I and XIII). The area so indicated is not by any means evenly covered with *Zostera*. In fact, many areas within this boundary which are several yards across may have but the barest sprinkling of this plant. Moreover, as is indicated on the map, there are numerous scattered or clustered and usually small plants of *Zostera* outside of this boundary.

In the more vigorous patches of *Zostera* found in the Inner Harbor in July, the individual plants often have a rhizome 0.33 meter long and from 2 to 3.5 or 4 mm. in diameter. It is made up of 15 or 20 internodes, and runs along horizontally 1 cm. or more below the surface of the mud. Each rhizome terminates in a floral shoot, and bears from 2 or 3 to as many as 5 or 6 leafy lateral shoots. These lateral shoots may branch two or three times above the

mud, each of these branches consisting of from 12 to 20 short internodes, and bearing from 4 to 8 functional leaves. The width of these leaves varies from 5 to 8 mm. and the longer of them are from 1 to 2 meters in length. The fertile, or floral, shoots of *Zostera,* at this season, vary in length from 50 cm. to 1.5 meters. Each consists of about 15 or 20 internodes, which are from 1.5 to 2 mm. in diameter and from 5 to 20 cm long. Each node bears a leaf which is about 4 mm. wide and 15 cm. long. On older parts of the shoot nothing is left of the leaves but the sheath and perhaps a small bit of the blade. Inflorescences in all stages of development are present on each fertile shoot, from floral rudiments just initiated at the top to spathes at the base from which the fruits have already been discharged.

The densest stands of *Zostera* seen in the harbor are that east of the channel to the Outer Harbor, northeastward from 1,200 north by 800 east, those along the two banks of the tide-stream from 2,000 north by 400 west to the depression at 1,500 north by 300 east, and that on an area of several hundred square yards extent southwest of the deep hole about 900 north by 200 east. On these areas there may be from 500 to 2,000 leaf-clusters of *Zostera* to each square yard of bottom. In other parts of the *Zostera* region indicated on the map, *e. g.,* in much of the area near the main north-and-south axis from 1,000 north to 2,000 north, the stand of *Zostera* is far less dense, with an average of 200 or 300 leaf-clusters per square yard. For some distance outside the indicated area, especially to the north and west, plants of *Zostera* are very infrequent, perhaps 20 to 100 small tufts to each square of the map, *i. e.,* to each 3,333 square yards.

These tufts are mostly scattered and show but 2 or 3 to 10 or 12 leaf-clusters each. The extreme limit of distribution of *Zostera* is shown on plate XIII by the use of the letter *Z,* which is used as a symbol for indicating the position of outlying plants. These plants are usually small, being 1.5 to 6 dm. from the rhizome to tips of leaves, and their distribution varies somewhat from year to year. For example, numerous scattered plants of *Zostera* were found at 2,000 north by 0 to 600 east in 1905 and 1906. From 1907 on, following the occupation of much of this area by beds of mussels (*Mytilus edulis*), *Zostera* has been nearly or quite wanting here. The presence of the mussels has evidently led to a gradual silting over of the bottom of this area, raising it to or above mean low water, which is probably a direct cause of the disappearance of *Zostera.* It may well be that the mussels also cause other changes in the soil, making it injurious to the *Zostera, e. g.,* in the content of such gases as air, CO_2, or H_2S. Such changes may explain the disappearance of *Zostera* from bottom not continuously occupied by mussels that has not yet been raised above the usual upper limit of this plant.

Though the horizontal distribution may seem decidedly irregular (plate XIII), especially the scattered marginal tufts, the distribution in depth is pretty constantly limited. It is found at levels extending from mean low water down to 3.5 feet below this. The parts of the harbor where *Zostera* occurs above the upper limit mentioned, are certain areas where bottom at 6 to 12 inches above mean low water is overflowed more or less at low tide by water from inflowing streams. For example, the southern prolongation of the *Zostera* area near 600 north by 400 east overlaps the mean low-water line very considerably, and scattered outlying plants of *Zostera* are found as far south as 300 north by 200 to 400 east or 275 north by 725 east, and even a few tufts near 210 north

by 500 east and at the 1.5-foot level. It seems evident from what has just been said that *Zostera* is excluded from bottom much above mean low water by its liability to death from exposure at low tide. In those places where it exceeds this usual upper limit it is protected from desiccation by water from streams, which runs over it at low tide.

The environmental factors determining the *lower* limit of the *Zostera* have not been distinguished with absolute certainty. So far as could be discovered, from a study of the relatively short lower margin of the *Zostera* area about the deep hole, this plant does not encroach on bottom lower than that indicated, because this lower bottom is sandy or shelly. Such soils, in this harbor, are nearly always bare, no matter what the depth. In the few places where *Zostera* seems to be growing on such bottom, the use of a sounding-rod usually shows that there is a softer subsoil of mud, an inch or two below the surface. It seems likely that the *Zostera* in these spots originally became established on a mud bottom which later, by some change in water-currents, was covered by a layer of sand and shell fragments. Only a few plants, which had very short, narrow leaves, were found growing on an apparently pure sandy bottom. Possibly the turbid water of this harbor may make the light supply inadequate at greater depths. In the clearer water of Casco Bay, Maine, *Zostera* grows on soft bottom 10 feet below low-water mark, also in Great South Bay, New York. A similar distribution of *Zostera* is found in Carmel Bay, California.

C. H. Ostenfeld (1909) has found a similar relative abundance and size of the *Zostera* (growing, however, in much deeper water), on sandy and on muddy bottoms of the coast of Denmark. He states (p. 33) that on the bare, firm, sandy bottom there is only a sparse growth of *Zostera* with short, narrow-leaved shoots, which are free from growths of epiphytic plants and of animals. On soft, muddy bottom, on the contrary, he finds a dense pure growth of *Zostera* with larger and broader leaves, which latter are occupied by many epiphytic diatoms, brown and red algæ, and various animals, *e. g.*, hydroids, mollusca, bryozoans, and ascidians. On pebbly bottom, where the interspaces between pebbles and boulders are occupied by softer soil, Ostenfeld finds a "mixed *Zostera* vegetation" in which, on certain areas, *Zostera* grows in the mud, while the pebbles give fixing-points for *Fucus, Laminaria,* and other coarse brown and red algæ. Another type of mixed *Zostera* vegetation is that mentioned by Ostenfeld as occurring in brackish waters with bottom of sandy mud, and is characterized by the abundance of the green algæ *Ulva, Enteromorpha, Cladophora rupestris, Chætomorpha linum* along with *Chara, Tolypella, Lamprothamnus,* and also the seed plants *Ruppia, Zannichellia,* and *Potamogeton pectinatus.* This last type is the one that approaches most nearly, on the whole, to the *Zostera* vegetation of the harbor we are studying. Perhaps the most striking difference between the two is the absence, from our area, of the Characeæ and *Potamogeton.* The similarity will be clear when we consider the distribution of the algæ of the harbor bottom.

In our harbor the differences in the character of the bottom, and so the presence or absence of *Zostera,* seem primarily due to the differences in the swiftness of the water-currents. The bottom of the deep hole, and of the channels north of it, is of sand or gravel and particles of shell, with a few bits of organic material, all of which may be seen shifting with the current when the tide is swiftest. The only fixed plants seen here were *Ceramiums,*

Polysiphonias, Rhabdonias, Ulvas, etc., which, with their anchoring pebbles, were evidently in transit through the Inlet. From a careful consideration of the conditions existing in the deeper portions of the harbor, it seems evident that the absence of *Zostera* is in some way determined by the swift tidal currents rushing over these portions. As there is no reason to believe that this current acts directly on the *Zostera,* it seems clear that the current acts by forming an unstable and sterile bottom on which *Zostera* can not establish itself. A merely sterile soil we would expect to be conquered by the gradual extension of *Zostera* into it, with an accompanying accumulation of organic matter about its shoots. We must conclude, therefore, that the downward spread of *Zostera* in this harbor is prevented by a shifting of the soil so frequent as to make it impossible for the out-pushing rhizomes to establish themselves and thus bind the soil.

Ostenfeld, in his study of *Zostera* in Danish waters, found that the shoots are perennial, and the leaves remain green all winter. The winter leaves of plants growing on mud bottom do not attain as great a length as leaves developed in summer.

A somewhat similar retardation of growth in winter seems to occur at Cold Spring Harbor. Since our observations were confined largely to the months of July and August, we can not speak with certainty concerning the activities of the *Zostera* in winter. On April 7, 1911, however, an abundance of *Zostera* plants was found with most of the leaves only 1 or 2 dm. long, and evidently young, but also with older leaves a half meter or more in length. Plants collected in about the same locality on July 11, 1911, had leaves 2 meters long. Many of these were dead and worn at the tip and seemed evidently more than 2 or 3 months old. Not many plants of *Zostera* were collected and measured in April 1911, but it seems probable, from the condition of the plants in the following July, that longer leaves would have been found by more thorough search in April. From all the evidence gathered we are led to conclude that while the longer leaves of *Zostera* plants may be torn off by waves and ice during the winter, the leaves of the more sheltered plants may often persist from fall to spring. This conclusion is strongly supported by the fact that the floral shoots certainly persist over winter. This is shown by the fact that floral shoots 90 cm. long and bearing fruits 3 to 4 mm. long were collected on April 4, 1913, by Dr. A. F. Blakeslee; also by the presence in early July of empty spathes on inflorescences which higher up bear mature and young fruits and unopened flowers. On the Danish coast, according to Ostenfeld, the floral shoots are initiated in April and drop off the rootstock in the late fall. We are not prepared to suggest any causal explanation for this difference in behavior of the *Zostera* in these two localities, unless it be the more destructive effect of winter waves in the more open water where Ostenfeld's plants grew.

In brief summary of the facts concerning the distribution of *Zostera* in the Inner Harbor, we can say *Zostera* commonly occurs on bottom between mean low water and 3 feet below this. In one or two areas flooded by streams at low tide, a dense stand of *Zostera* may grow on bottom a few inches above mean low water. The extreme upper limit at which *Zostera* was found—a few plants only—is 1.5 feet, and the extreme lower limit is —4.5 feet. The species is almost entirely confined to muddy bottoms.

The part played by *Zostera* as a substratum for epiphytic algæ will be noted in discussing the distribution of the algæ.

Ruppia maritima: This comparatively diminutive and delicate species is the only seed plant besides *Zostera* that is found on the bottom of the Inner Harbor below 1.5 feet. The characteristic mature plant of *Ruppia,* as it occurs in this harbor, is about 25 cm. long, and of 10 to 12 internodes varying in length from 20 to 70 mm. It has 8 to 10 functional leaves each 20 to 60 mm. long and 1 mm. wide. The plants flower freely at Cold Spring Harbor during July and August, but the stalk of the infloresences is short, rarely more than a few cm. long, and therefore the flowers are not at the level of the water-surface except for about half an hour at the rise of the tide and a like interval at its fall, *i. e.,* when the water-level is between 6 inches and 1.5 feet above mean low water. The plants flower and apparently fruit freely, as seedlings are rather frequently found.

While *Zostera* is characteristic of an area lying below mean low water, *Ruppia* is practically confined to a vertically narrow belt between mean low water and 1.25 feet. The extreme limits are —0.5 foot and +1.5 feet. Though the vertical distribution of *Ruppia* is thus very limited, its horizontal distribution is quite wide. At its lower limit, near mean low water, *Ruppia* is found mixed with scattered *Zostera,* but it is also scattered abundantly over areas near the 1.5-foot level, where *Zostera* is entirely wanting, *e. g.,* 1,300 to 1,600 north along the east shore. Nowhere does the stand of *Ruppia* become as dense as the denser stands of *Zostera,* and, in fact, areas where the bottom is actually covered by *Ruppia* are small and rare. This is due not only to the relatively small number of plants, but also to their delicacy.

The areas where *Ruppia* is most abundant are those with a soft bottom, bare of *Ulva* and usually protected from currents and waves. Such areas are those indicated on plate XIII. They are found chiefly in the western and northern parts of the harbor, but there is another such habitat with abundant *Ruppia* along the eastern shore behind the *Zostera* belt. The horizontal distribution of *Ruppia* is, in other words, limited to areas of quiet water and the fine, muddy soil formed in such areas. The vertical distribution of *Ruppia,* on the other hand, seems clearly determined by tide-levels. The lower limit of this species, as we have seen, is mean low water, or a few inches lower in exceptional cases, and the upper limit is at 1 foot, or more rarely at 1.5 feet, above mean low water. That is, the plant never occurs where constantly submerged, but rather on areas which are exposed for from 0 to 4 hours each day, depending on the magnitude of the tide. It seems clear that competition with other species can not be an important factor in keeping *Ruppia* out of soils at lower levels, since *Ruppia* does not occur on bottom below mean low water that is bare of *Zostera* and *Ulva.* The character of this bottom is apparently identical with that on which *Ruppia* is growing a foot or two higher up. There seems to be no difference in the conditions at these two levels, except in the relative duration of submergence and exposure.

The upper limit of distribution of *Ruppia* may be determined in part perhaps by competitors, *e. g., Spartina glabra,* in the shade of which *Ruppia* occasionally grows at its upper level. It seems more probable that *Ruppia* does not flourish above the 1-foot or 1.5-foot level because unable to withstand the exposure to desiccation by air and sun at low water. This view is supported by the fact that *Ruppia* is most abundant in areas where it is kept wet by little rivulets that run over the mud at low tide, *e. g.,* along the edge of the tide-stream at

2,000 north by 200 to 400 west. The same is true even if the water moistening the plants at low tide is fresh water, *e. g.*, at 1,300 to 1,600 north by 1,000 to 1,075 east, or near the mouth of the creek at 200 north by 400 to 600 east.

B. ATTACHED ALGÆ OF THE HARBOR BOTTOM (THE "LITHOPHILOUS BENTHOS").

Under this head we include algæ attached to stones, shells, or stakes below the 1.5-foot level, the "Lithophilous Benthos" of Warming. Many specimens of these same species may be broken off and found drifting about the harbor entirely free of any support. Though 18 or 20 species of algæ may be found on the bottom of the harbor, only 7 or 8 of these, including the *Ulva* and *Enteromorpha clathrata* mentioned above, occur in any considerable numbers. Even these are not at all abundant except in the Inlet, or, in the case of three or four species, along the streams entering the harbor.

The species that have been found on the bottom at one time or another are: *Beggiatoa mirabilis, Oscillatoria* sp?, *Cladophora (expansa?), Enteromorpha clathrata, E. intestinalis, Ulva lactuca, Ascophyllum nodosum, Ectocarpus siliculosus* var. *amphibius* Harv., *Fucus vesiculosus, Pylaiella littoralis, Scytosiphon lomentarius, Agardhiella tenera, Callithamnion roseum, Ceramium rubrum, Chondria tenuissima, Chondrus crispus, Dasya elegans, Delesseria leprieurii, Gracilaria multipartita, Grinnellia americana, Hildenbrandia prototypus* Nardo, *Petrocelis cruenta, Polysiphonia variegata, Porphyra laciniata.*

In discussing the occurrence of these algæ we may take up in some detail the distribution of the more abundant species in each class, and then note briefly the information that we have been able to gather concerning the occurrence of the rarer or occasional forms.

SCHIZOPHYTA.

Beggiatoa mirabilis occurs commonly on the surface of the black mud of the bottom, from below mean low water up into the present belt, and also, as we shall see, still further up, to the 6 or 7 foot level, in tide-pools, or in trickles of salt water at the edge of the æstuarial marsh. *Oscillatoria* sp? was found only infrequently coating the surface of dead fronds of *Fucus* in the Inlet, at about mean low water.

CHLOROPHYCEÆ.

Of the green algæ enumerated above we have already noted the distribution of attached plants of *Enteromorpha clathrata* (p. 21) and *Ulva* (p. 18). The only remaining species are *Cladophora* (*expansa?*), *Enteromorpha intestinalis*, and *Ulothrix flacca.*

In April 1911 tufts of *Cladophora* (*expansa?*) 3 or 4 cm. long were found frequently along the Inlet near mean low water at 1,800 to 2,000 north. In September 1911 similar tufts were frequent in the creek, at 200 south, between the 1 and 2 foot levels. Considerable mats of it are found each summer tangled with *Zostera* and with other algæ in the middle of the harbor bottom, where it also occasionally appears as an epiphyte on *Zostera* (plate VIII). At this season it is much more abundant at higher levels, as we shall see later.

The large, simple, tubular fronds of *Enteromorpha intestinalis* are likewise characteristic of higher levels, especially in the neighborhood of fresh-water streams. Along these streams, however, when they are large enough to reach to the low-tide mark as single streams, we sometimes find the *Enteromorpha* accompanying them downward to within the limits of our zone. For example, at 20 south by 590 east, beside the main stream at the head of the harbor, at the 1.5-foot level, *E. intestinalis* is usually quite abundant and of good size, though neither as abundant nor as large as it is, at somewhat higher levels, a few feet south of this. A very interesting patch of this *Enteromorpha* is that growing on the bottom near 1,440 north, on the east shore. At this point the overflow pipe from an artesian well penetrates the wall of the wharf at the 4-foot level. At low tide the water from this pipe falls to the bottom, which is at about the 1.5-foot level, where the water splashes down upon pebbles and stones, and then runs off over the bottom toward low-water level. A circle of the bottom 4 feet in diameter, round about the point where this stream strikes, is covered by hundreds of plants of *Enteromorpha intestinalis,* from 5 to 20 mm. in diameter and 2 or 3 dm. in length. A few dozen plants are found scattered along the stream running from this circle down over the bottom, but this latter area is dominated by *Ascophyllum.* Near another fresh-water outlet 100 feet north of this we have a similar sparse sprinkling of this *Enteromorpha* which does not dominate any appreciable area. The factors affecting the distribution of *Enteromorpha intestinalis* will be mentioned in discussing its distribution at higher levels, where it is more abundant.

Ulothrix flacca was found but sparingly below the 1.5-foot level in April 1911, though it was everywhere abundant just above this.

PHÆOPHYCEÆ.

Ascophyllum and *Fucus:* What has just been said of the relative abundance of *Enteromorpha* in this belt is true also of *Ascophyllum* and its relative *Fucus,* two genera which, because of their similarity of distribution, may be discussed together. These algæ attain their greatest abundance in the next higher belt of vegetation, in the harbor, from 1.5 to 6 feet. (See plate IX.) The relatively few plants found below the 1.5-foot level grow on stones, chiefly along the channel to the Outer Harbor or along that from the Creek. Occasionally plants or clumps may be found on stones or sunken logs along the shores of the harbor. Near the middle of the harbor these algæ are rarely found, and then they are attached to small pebbles or shells which they have evidently dragged with them from higher levels in the Inlet.

From the distribution of *Fucus* and *Ascophyllum* found in the Outer Harbor, it is evident that these plants may grow abundantly at, and somewhat below, low-water mark. It is therefore probable that the sparseness of these algæ below the 1.5-foot level in the Inner Harbor is due in part to the absence below the bases of the wharves of any proper substratum for their attachment. The abundance of shifting *Ulva* is another important factor, for these sheets would be sure to bury the relatively slow-growing rockweeds before they could attain any considerable size.

Ectocarpus siliculosus var. *amphibius:* This form has been found below the 1.5-foot level in only one locality, near a deep portion of the channel of the

main stream, at 150 south by 780 east. Just upstream from this depression (160 south), the pebbly bottom slopes sharply down from a 1.5-foot level to —0.5 foot in the deepest parts of the depression, and then rises to about 1 foot at the northern end of the hollow. In the bottom of the deepest part of this depression, and still more abundantly in the little rapids above it, the *Ectocarpus* grew in luxuriant tufts, with numerous gametangia, in the early summer of 1911. In late August of this same year it had practically disappeared. The water flowing over this alga during 3 to 5 hours of each tide, or 6 to 10 hours per day, is entirely fresh, while for the remainder of the tide the plants are surrounded by salt water. Moreover, the change from one to the other is quite rapid, which shows that the alga is capable of withstanding marked and sudden changes in the osmotic quality of the surrounding medium.

Scytosiphon lomentarius: This alga occurs in the Outer Harbor all summer and unattached small tangles of it are found scattered over the bottom of the Inner Harbor at this same season. Only in early April 1911 did we find it attached in the Inner Harbor. At that time it was sprinkled in frequently among *Ulva, Enteromorpha clathrata, Porphyra,* and *Pylaiella,* on the stony bottom east of the channel of the Inlet, at 1,900 to 2,100 north and from mean low water up to the 1-foot level. These plants were 30 cm. long, about 1 mm. in diameter, and were fruiting.

Pylaiella littoralis: This densely branched filamentous brown alga has been found nearly every summer at one or more spots about the harbor. It is usually present, for example, in the deeper part of the Creek at 150 south at —0.5 to +1.5-foot levels. It was abundant in the Inlet in July 1912, but had largely disappeared by September. It is sometimes found also on the shady sides of piles or stones on the wharf of the Research Laboratory, chiefly, though not wholly, above 1.5 feet. In 1912 large tufts grew where splashed by fresh water at 150 north and 500 north on the west shore. In April 1911 this alga was probably the most abundant species about the harbor from mean low water up to 3 or 4 feet. At half tide its dense tufts could be seen everywhere, often as much as 1.5 dm. long. They were attached to pebbles, shells, stones, wood, and even tangled among the stalks of the *Spartina glabra* at its lower levels. All of these plants were either sterile or had chains of zoosporangia. On September 29, 1911, this same alga was found on pebbles in the deep part of the main stream at 150 south and in the rapids just above this at 200 south. In the plants collected at this time the only reproductive organs seen were gametangia, which had not been seen at all on plants collected in April or in midsummer.

From what we have noted it is clear that *Pylaiella,* like *Ectocarpus siliculosus,* is capable of enduring the rapid change from salt to fresh water and the reverse which occurs in the main stream with each change of tide. It is also noteworthy that while this alga is very abundant and widely distributed about the harbor in April, it is represented in summer by only a few groups of plants in areas protected from high temperature and desiccation. The fact that the plants found in spring and early summer bore zoosporangia only, while those found in September bore only gametangia, suggests the probability that this alga really has a distinct seasonal alternation of a spore-bearing period with a gamete-bearing period. It may even prove to be an alternation of distinct asexual

and sexual generations, comparable with that of *Dictyota* and that of the red algæ *Polysiphonia* and *Griffithsia*. (See Lewis, 1914.)

The vertical distribution of *Pylaiella* thus far recorded extends from −6 inches up to 5 or 6 feet. That is, it occurs both in areas where it is nearly always submerged and also, on shady spots along wharves, where it is exposed to the air from 8 to 9 hours each tide. It seems evident that this alga is not able to go higher on the wharves, nor, in most places, even as high as here recorded, because of the danger of desiccation during low tide. It perhaps does not grow on bottom below mean low water at the Inlet because of the swift current which runs over the bottom, sweeping along pebbles, shells, and dislodged algæ. Why, if it can endure long submergence in fresh water, it does not push further up the fresh-water streams, it is not easy to understand, unless it be its inability to endure continuous submergence in fresh water. *Pylaiella* would probably prove a good subject for experimental determination of the effect, on the distribution of algæ, of such conditions as high temperature and exposure to fresh water and to dry air.

The Rhodophyceæ.

Of the 13 species of this group of algæ growing on the bottom of the harbor, the most important are *Chondrus, Porphyra,* and the incrusting alga *Hildenbrandia*. We will discuss these first, and then take up the remaining forms in alphabetical sequence. Plate IX shows the distribution of the most frequent of the Rhodophyceæ about the harbor.

Chondrus crispus is usually the most abundant red alga in the harbor, after the *Ceramiums, Hildenbrandia,* and perhaps *Bostrychia*. It occurs abundantly in the Inlet during the summer, chiefly on the pebbly bottom east of the channel, between 1 foot below and 1 foot above mean low water. In July 1911, for example, *Chondrus* was distributed over a strip varying from 10 to 40 or 50 feet in width, and stretching from 1,700 to 2,000 north. The plants found here are from 0.5 dm. to 1 dm. in height, and form dense tufts of a reddish or brownish color. They are apparently quite as vigorous and fruit quite as freely as plants growing in open water in the Outer Harbor or in Long Island Sound. Two or three smaller plants were found at 1,600 north near mean low water. These were the southernmost plants ever recorded. Though this alga is one of the most constant in occurrence and distribution during each summer, it could not be found after careful search along the Inlet in April 1911. On September 28, 1911, this species was not seen, though searched for as carefully as possible, when the water was at the +1-foot level.

Porphyra laciniata: This is the only red alga found on the bottom of the harbor in April 1911. It was then nearly as abundant and widely distributed as *Ulva,* except that it was never found in or near fresh-water streams. The *Porphyra* was then most abundant east of the channel to the Outer Harbor, from 1 foot below to 1.5 feet above mean low water. The individual plants at this point were often 2 to 3 dm. long, and about as broad. In other parts of the harbor, in April, the *Porphyra* is sprinkled about somewhat generally, though not abundantly, chiefly on wharves and wrecks between the 2-foot and the 4-foot levels. Hundreds of sheets of this alga, usually 1 to 2 dm. across, but sometimes larger, were seen in April among the stubble of the *Spartina glabra* along the west shore. Closer examination showed that the vast majority

of these were detached, only a few dozens of them being attached to mussels. The only source that could at this time be discovered for such numbers of the plants of *Porphyra* was the dense colony of them in the Inlet. With so many detached plants about the harbor it is interesting to note that they do not settle on the bottom to cover large areas, as *Ulva* does. This is evidently because the *Porphyra* floats and is therefore cast up on the beach instead of settling. *Porphyra* is noticeably free from epiphytes, probably because of its lubricous surface.

In the summer *Porphyra* is relatively rare in the Inner Harbor, though it is still abundant at various points in the Outer Harbor. The plants found in our area in summer are chiefly on the wharves, between 2 and 4 feet, and their distribution at these levels will be noted in discussing the rockweed association.

The factors determining the distribution of *Porphyra* are not very clearly indicated by its occurrence in the area under observation. The limits noted in April and July, *i. e.*, —1 to +4 feet, are very nearly the limits of distribution of the plants found on the open shores of Long Island Sound. From the observations here made it seems evident that cool water, stirred by waves or tidal currents, furnish the conditions favoring the growth of *Porphyra*. The upper limit seems to be determined by the time of exposure to the air, and the lower limit probably by the lack of light due to the turbidity of the water. It seems hardly probable that a delicate alga of a single layer of cells can be confined to levels above low tide, because of the need of exposure for aeration.

Hildenbrandia prototypus, an incrusting species, is more widely spread in summer than any other red alga of the Inner Harbor. It occurs on pebbles and stones at all levels from mean low water up to 6 or 6.5 feet and wherever there is a proper substratum. It grows both in pure salt water and in places where the plants may be overflowed for several hours at each tide by fresh water. For example, it is found abundantly on pebbles along the channel to the Outer Harbor from mean low water up to 1.5 or 2 feet, and on the shoals beside the Creek, at 470 east and 625 east at 1 to 2 feet, and, finally, it occurs within the present belt on stones of the wharf of the Research Laboratory, and of the wharves east of the Inlet at 2,200 north to 2,600 north. The distribution of this alga at higher levels and the factors determining its upper and lower limits will be discussed in describing the next higher belt of vegetation.

The remaining ten species of Rhodophyceæ found on the bottom of the harbor are usually represented by few dozens or scores of individuals each. In fact, one or more of the species may be entirely wanting in some summers. Some of these ten species may develop *in situ*, on stakes or buoys, or on stones of the bottom. Others are rarely found fixed to a stable substratum. More often they are found drifting about over the bottom, being either entirely free or dragging about with them small pebbles or shells which hold the young plants in place, but which are too small to anchor securely the now full-grown plants. The ten species to which we have referred are: *Agardhiella tenera, Callithamnion roseum, Ceramium rubrum, Chondria tenuissima, Dasya elegans, Delesseria leprieurii, Gracilaria multipartita, Grinnellia americana, Lomentaria uncinata,* and *Polysiphonia variegata*. Of these algæ *Callithamnion* and *Lomentaria* have each been found during one season only, when a considerable number of plants of each were established in the Inlet, near 2,300 north by 1,175 east, at about mean low water.

Agardhiella is a coarse and rather cartilaginous species which is found abundantly in parts of the Outer Harbor and which often drifts into the Inner Harbor. It has not been found within our limits fixed to anything larger than small pebbles which are dragged about by the stiff, bushy plants. In some seasons dozens of these, and still larger numbers of entirely free plants, are tumbled about over the bottom, below the 1.5-foot level.

Ceramium rubrum is abundant on *Zostera* in the Inner Harbor and is also found occasionally on pebbles or shells in the Inlet at 2,300 north by 1,000 to 1,200 east at mean low water and below. Its relative, *C. strictum,* has not been found, except on *Zostera.*

Chondria also has been recorded but once since our work began (in July 1908), though it was often seen in earlier years in the same place,—2,200 to 2,300 north, on the east side of the Inlet, at about the —1-foot level. In the one case recorded carefully the plants were about 1 dm. high, and all of them were tetrasporic. During the early years of this study *Chondria* was abundant in the Outer Harbor just outside the Inlet. At these times floating plants of *Chondria* were common in the Inner Harbor. The fixed plants outside the Inlet have disappeared almost completely during the last few years, and with them, of course, the free plants in the Inner Harbor. No cause has been discovered to which this disappearance of the *Chondria,* and of other red algæ also, can be attributed with certainty. It seems probable that it is related to the sudden covering of large areas of the bottom by mussels which occurred in 1907.

Perhaps the greater rarity of certain algæ of the Inner Harbor in recent years is due to the greater distance over which the spores must come from areas outside it, where the plants are abundant and constantly present. It seems evident that fewer of the spores can reach the Inner Harbor from an area 2 or 3 miles away than from one 200 or 300 yards away, though as a matter of fact we have no certain evidence of the endurance of these spores or of their ability to remain afloat for so long a time.

Delesseria is a smoky green, inconspicuous alga that has been found only once within the limits of the belt that we are discussing—at 1,750 north by 1,070 east at the 1-foot level. It is more frequent at slightly higher levels, as we shall see later.

Gracilaria is found in small numbers attached to pebbles and shells at levels between —2 and +1.5 feet on the bottom of the Inlet. It is sometimes also found being washed about over the bottom of the harbor, either entirely free or else dragging about with it the small pebble or shell on which it has grown. Both attached and free plants of *Gracilaria* have become less frequent of late years, probably for reasons identical with those suggested in speaking of *Chondria.*

Grinnellia is a broad, sheet-like alga which is quite frequent in the Outer Harbor. When our work began attached plants of it were abundant every summer in the shallow branch of the Outer Harbor directly north of the Inlet. In 1906 three or four attached plants were found near 175 north by 625 east. These in all probability had been carried in by the tide and had dragged their small supports with them. Our records for 1907 show that half a dozen attached plants of this species were found in the Inlet between 2,200 and 2,400 north near mean low water. Plants which are entirely free are still found drifting over the bottom of the harbor, but while in earlier years these could be seen by

the score, in 1909 and 1910 only a dozen or fifteen could be found in the whole harbor. Not half a dozen attached plants have been seen in the Inlet or Inner Harbor during the past two years. The filling up of the area of the Outer Harbor just north of the Inlet, which is correlated in some way with the abundance of mussels, has driven *Grinnellia* out of the area where it was formerly abundant, and from which the Inner Harbor could be readily supplied with spores and drifting plants. It is clear that in this, as in the case of the other red algæ mentioned, we can not know with certainty the explanation of their distribution in the summer until we know more of their distribution and activities during the other seasons of the year.

Polysiphonia is abundant in some seasons on pebbles on the bottom of the Inlet from 2,000 to 2,600 north, between mean low water and —3 feet. Tetrasporic plants are common in summer, while cystocarpic and antheridial ones are usually rare. In late September 1911 this alga was far more abundant than it has ever been in midsummer on the bottom of the east side of the Inlet from mean low water downward. In the region between 2,000 and 2,200 north, which was most carefully examined at this time, there were often 10 to 15 dense tufts to each square meter. All of these plants that were examined proved to be sexual, chiefly cystocarpic. In most summers a few drifting plants of *Polysiphonia* are found in the Inner Harbor, some of them attached to small pebbles. In other summers these and the attached plants of the Inlet are practically wanting. When, therefore, we find in some succeeding summers a relatively large number of these plants in the Inlet, we are inclined to conclude for this species, as for the others mentioned above, that the new plants must come from spores brought in from the Outer Harbor, rather than from any perennating portions of plants of a former summer left in the Inner Harbor. The great abundance of this species in September 1911, however, suggests the possibility that its basal portions may be constantly present, but that its shoot is well-developed only in occasional summers, when conditions are unusually favorable at that season.

The free or drifting plants of the red algæ of the Inner Harbor that have been noted above may in some species remain in the living condition but a short time. Such, *e. g.*, is usually the fate of the *Ceramiums, Chondria, Dasya,* and *Polysiphonia.* Other species, on the contrary, like the green algæ *Cladophora* and *Enteromorpha,* may persist indefinitely and even continue to develop. Thus, *e. g.*, when *Agardhiella, Gracilaria,* and *Grinnellia* lodge on the bottom near low-water mark, they may continue to produce tetraspores or cystocarps for weeks after being torn loose from their substrata. In this way, of course, spores of algæ not before growing in the harbor may be dispersed about it in considerable numbers.

C. EPIPHYTIC ALGÆ ON ZOSTERA AND ULVA.

About 7 or 8 species of the algæ of the Inner Harbor are attached to other plants, chiefly to *Zostera.* In fact, it is the presence of *Zostera,* to serve as a substratum, that alone makes it possible for most of the epiphytic species to grow at all abundantly in the Inner Harbor. It is because of this importance of *Zostera* as a substratum that we have indicated its distribution on our topographic map of the harbor.

The species of algæ which frequently occur as epiphytes on *Zostera*, on *Ulva*, or occasionally on other algæ, are the following: *Spirulina tenuissima*, *Cocconeis scutellum*, *Melosira borrei*, *M. nummuloides*, *Navicula grevillei*, *N. kennedyi*, *Synedra affinis*, *Cladophora (expansa?)*, *Enteromorpha clathrata*, *Ceramium rubrum*, and *C. strictum*. (See plates VIII and IX.)

Among these epiphytic forms there is no general predominance of any one species, though because of their size and color the *Ceramiums* may be more prominent. We may therefore discuss the species enumerated in alphabetical order within each class, beginning with the simplest.

Schizophyceæ.

Spirulina tenuissima: This alga, as we shall see later, is widely spread from mean low water up to the 7-foot level, but it is in the present belt, as an epiphyte on *Zostera*, *Ulva*, and sometimes on *Enteromorpha clathrata*, that it is most luxuriantly developed. On the *Zostera* this alga sometimes forms dense yellowish-green patches, sparkling with gas-bubbles and often many square decimeters in extent. For example, in 1910, patches of this sort were thickly sprinkled over hundreds of square meters of bottom from 1,300 to 1,500 north by 950 to 1,050 east, covering one-third of the *Zostera* plants and matting scores of their leaves together. Similar, though usually smaller, patches of *Spirulina* have been seen adhering to the large sheets of *Ulva* or on tangles of *Enteromorpha clathrata* in the southeastern parts of the harbor. Still smaller patches occur occasionally on stakes or buoys in the middle of the harbor. These patches of *Spirulina* are 5 to 10 mm. thick and practically pure, showing but few other organisms within the mass, such as filaments of an *Oscillatoria* or of some other epiphyte of *Zostera* buried by the growth of the *Spirulina*. These dense growths of *Spirulina* are confined, in this harbor, to levels within a foot or less of mean low water. At higher levels, up to its upper limit at about 7 feet, *Spirulina* occurs sparingly mixed in mats or felts with numerous other Cyanophyceæ, none of which seem to flourish near mean low water, where *Spirulina* does best. The lower limit of *Spirulina* in this harbor is about 1 foot below mean low water, and it is apparently conditioned by the presence in somewhat quiet water, which gets warm at low tide, of a substratum such as *Zostera* or *Ulva* over which it may spread. In its occupation of substrata at higher levels it is restricted probably by the danger of desiccation, except in shaded areas or where it is protected by mats of other algæ. Probably at higher levels also, in some localities, it is kept lower than usual because of lack of a suitable substratum.

Bacillariales.

The epiphytic Diatomeæ of the bottom of the harbor include the most abundant and widely distributed epiphytes of this belt. *Cocconeis scutellum*, *e. g.*, is found, often in great numbers, on nearly every plant growing in the Inner Harbor. It grows not only on *Zostera*, but even more abundantly on *Ulva* and on both attached and free plants of other larger algæ. It is often especially abundant on the epiphytic *Ceramiums*. The distribution of this diatom has not been studied in great detail, but it apparently occurs on all living substrata throughout the harbor, except near fresh water. In vertical distribution *Cocconeis* is found from —2 feet to +1.5 feet.

Melosira borrei and *M. nummuloides:* These diatoms, though less abundant, are even more widely distributed over the harbor-bottom than *Cocconeis,* since they endure submergence, for several hours at least, in entirely fresh water. They are best developed, however, on the long leaves of *Zostera* or on stakes or buoys in the middle of the harbor. Here they form tufts of a rusty brown color from 2 or 3 to 25 or 30 mm. in diameter and from 4 or 5 to 25 or 30 mm. in length. The distribution of these tufts is somewhat more restricted than that of *Zostera.* They are present in considerable numbers only on the larger, denser *Zostera* near the center of the harbor. On outlying *Zostera,* as well as on *Ulva, Enteromorpha, Pylaiella,* and on several of the Florideæ of the bottom, *Melosira* is found in single threads or clusters of few short filaments. Apparently all these *Melosira* tufts of the bottom and those along the Creek to 200 south are of the same species and are identical with those which occur mixed with Cyanophyceæ and Chlorophyceæ on marsh and beach at higher levels. The distribution of *Melosira* tufts is limited primarily by that of the plants on which it grows. It is evident, however, that though *Melosira* does not grow in the swiftest currents, it is most luxuriant where there is a considerable movement of the water, *e. g.,* at the sides of the deeper channel leading from the Inlet toward the Creek and near the tide-stream entering the deep hole from the northwest. The abundance of *Melosira* on the *Zostera,* just aside from the swiftest current, where the Inlet opens into the Outer Harbor, confirms the conclusion that frequent change of the surrounding water is distinctly advantageous for this diatom.

Navicula grevillei and *N. kennedyi:* These species have much the same distribution as *Melosira* in the middle of the harbor, and are even more abundant and more luxuriant than *Melosira* on the denser *Zostera.* The tufts of these *Naviculas* are distinguishable from those of *Melosira* by the somewhat lighter color, the slippery feel, and the abundant branching, as well as by the iridescent character of the gelatinous matrix in which the frustules are embedded.

Synedra affinis: This is another diatom which is widely distributed on many hosts. It was especially abundant on *Pylaiella* in the Inlet on April 8, 1911, and on *Pylaiella* and *Enteromorpha intestinalis,* in the Creek at 200 south in September 1911. On many branches of the *Pylaiella* these diatoms stand out so thickly as to make these branches look like diminutive chenille cords.

There are of course other epiphytic diatoms (see list on p. 161), but those mentioned are the most abundant and widespread in distribution.

CHLOROPHYCEÆ.

The only important epiphytic Chlorophyceæ are *Chætomorpha ærea* forma *linum, Cladophora (expansa?),* and *Enteromorpha clathrata.*

Chætomorpha ærea: Though this is originally epiphytic, it is found most frequently lying on the *Ulva* or tangled with *Zostera, Cladophora,* or *Enteromorpha* on the bottom, near the middle of the harbor. What is apparently the same species is found at higher levels among the *Spartina glabra.*

Cladophora (expansa?): This is a species which is rather frequent in little tufts attached to *Zostera* near the deep hole, though far less abundant than its fellow-epiphytes *Enteromorpha clathrata* and the two *Ceramiums.* The tufts of *Cladophora* are 2 or 3 cm. long and are made up of repeatedly branched and densely interwoven filaments.

Enteromorpha clathrata: The occurrence of this species as an epiphyte we have already mentioned when referring to the long, streaming tufts of it on the *Zostera* as the source of the loose mats of this alga that drift over the bottom. We may here emphasize the fact that it is very abundant as an epiphyte. Often a dozen large tufts of it may grow on a single leaf-cluster of *Zostera,* and the filaments may attain a length of several decimeters before being set free, which usually occurs by the rupture of the supporting leaf. *E. clathrata* also has a wide distribution. It is the only noticeable epiphyte on the outlying clumps of *Zostera,* except a few tufts of *Melosira.*

RHODOPHYCEÆ.

As indicated in our enumeration of species, only two epiphytic red algæ have been found in the harbor, and both belong to the genus *Ceramium.* Though *Polysiphonia* occurs as an epiphyte on *Zostera* in other Long Island waters, mature plants of this species never have this habit in our harbor. *Melobesia,* another epiphyte found in more saline waters about Long Island, does not occur here at all.

Ceramium rubrum: This alga forms dense tufts, 5 to 10 cm. long, on the leaves of *Zostera.* Dozens or scores of these large tufts may sometimes be seen on each square meter of the *Zostera,* and in such areas this *Ceramium* is the most prominent epiphyte. This alga is most abundant just aside from the swiftest current along the Inlet, about the deep hole, and beside the tide-stream entering the latter from the northwest (plate IX). Evidently this red alga, like *Melosira,* flourishes best in moving water. In fact, the *Ceramium* fails to accompany the *Zostera* to the limit of its distribution, the outer or upper third of the *Zostera* being bare of the alga. Some of the plants of this *Ceramium* found in July and August bore tetraspores and others cystocarps or antheridia.

Ceramium strictum: This is the only red alga of the Inner Harbor which has been found here solely as an epiphyte. It is somewhat smaller in size and brighter in color than *C. rubrum.* The distribution of *C. strictum* is in general similar to that of *C. rubrum,* but it is evidently still more closely confined to the *Zostera* immediately surrounding the deep hole and the tide-stream flowing into it from the northwest.

So far as has been determined from a study of the epiphytic algæ of the harbor bottom, a study which has been concerned especially with the *Ceramiums,* these algæ are found at levels where they are submerged at all but the lowest tides. They evidently will not endure long exposure to dry air. The absence of the *Ceramiums* from the *Zostera* growing in the area from 500 to 700 north by 200 to 600 east indicates that these algæ can not endure submergence in the brackish, and for part of the time actually fresh, water which flows from the Creek at low tide.

3. THE MID-LITTORAL BELT (1.5 TO 6.5 FEET).

As one looks about the harbor at low tide the whole natural shore for some distance below high-water level is seen to be occupied by a very clearly marked belt of vegetation of quite uniform character. Closer examination shows that the sole conspicuous plant of this green belt is the salt reed-grass *Spartina glabra* var. *alterniflora,* and that it really occupies the middle portion of the strip of muddy shore between the two tide-marks. In fact, except where

A. Lower Edge of Zone of *Spartina glabra*, near 2,200 North × 500 East, with *Fucus vesiculosus spiralis*.

B. Wall, at 1,600 North on East Side, with Upper Part of Belt of *Fucus* and *Ascophyllum*.

A. South Shore of Spit looking Eastward from 100 West, showing Upper Margin of *Spartina glabra alterniflora* (at right), *Suæda* (in center middle distance), and at left *Ammophila*, *Solidago*, and *Ailanthus*. The tide stakes are at 7, 8, 9 and 10 feet respectively.

B. Portion of East Shore just South of Mill (400 to 500 North), showing *Spartina glabra alterniflora* and *Scirpus americanus* (left foreground). *Sambucus* and *Ailanthus* (center background), *Solidago sempervirens* and *Iris versicolor* (right foreground and middle distance).

local conditions of soil-moisture or shade are unusual, this grass is confined to levels between 1.5 and 6.5 feet. On the mud with the *Spartina* are found one other seed plant, *Lilæopsis,* and numerous algæ, mostly small and inconspicuous, except where matted together in numbers.

If the observer now turns to the portion of the harbor's edge bounded by wharves, he finds the stone walls and piles between tide-marks occupied by a belt of brown rockweed. Closer examination of these areas shows that they also are generally confined between the 1.5 and 6.5-foot levels, and that, though numerous other algæ may be found here, the areas are dominated by the rockweeds *Ascophyllum* and *Fucus.*

These two types of vegetation, found between 1.5 and 6.5, we may designate as the Mid-littoral Marsh and the Mid-littoral Rockweed Association respectively. Together they bound practically the whole circumference of the harbor. The only breaks in this distinct belt or zone are the stream-beds and two or three short stretches of artificial gravel beach.

A. THE MID-LITTORAL MARSH.

This belt, as has just been indicated, is a Spartinetum, dominated completely in most areas by *Spartina glabra.* It evidently corresponds in many respects to the "salt-reed swamp" of Warming (1909, p. 223). There are two striking features of this marsh at Cold Spring Harbor. In the first place, there is no admixture of other seed plants save half a dozen small patches of *Lilæopsis* and a few scattered migrants from the next higher belt, which wanderers, except near fresh-water streams, never get more than a few inches below the 6-foot level.[a] In the second place, this *Spartina* lies exactly in the middle of the "littoral region," if, with Kjellman (1877, p. 57) or Oltmanns (1905, p. 167), we define this region as that lying between the two tide-marks. Kjellman chooses the extreme upper and lower tide-marks as the boundaries of this littoral zone, on the west coast of Nova Zembla. But at the place where he worked the range of tides is small and the maximum range differs but little from the mean range. In the harbor we are dealing with the mean tide-limits have been chosen as boundaries for the littoral belt because the extreme range of tides is much greater than the mean, and because this choice gives us a belt characterized by distinct vegetational types.

At Cold Spring Harbor, where mean high water is about 8 feet above mean low water, and where the Spartinetum lies between 1.5 and 6.5 feet above mean low water, this association seems very aptly named the Mid-littoral Marsh. Moreover, from observations made elsewhere on Long Island and on Casco Bay, Maine, we are led to believe that the salt reed-grass along our whole North Atlantic coast will be found to be located just about midway between the mean tide-marks. We believe the name here used may be found generally applicable and clearly descriptive, for this *Spartina* association, wherever its vertical distribution is accurately determined.

In our detailed discussion of the vegetation of the Mid-littoral Marsh we will first consider the distribution of the *Spartina* and the other seed plants that are associated with it in its upper portions, and then take up the distribution of the algal felts or tangles and more scattered algæ which form "subordinate communities" on the bottom between these seed plants.

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[a] *Scirpus nanus* also has been seen below the 6-foot level in a few places on the Marsh.

1. The Spartina Glabra Association.

In discussing the character and distribution of this association it will be best, because of the differences in their nature, to take up the north shore separately from the east, west, and south shores. Nowhere else about the harbor does the *Spartina* association assume such prominence as along the south side of the Spit, which stretches across the north end of the Inner Harbor. We may therefore legitimately regard this as the highest development of the *Spartina* association and discuss in this connection not merely the distribution of the *Spartina* in this particular area, but also the general vegetative and reproductive characters always shown by this grass wherever found. The area occupied by *Spartina* on the Spit is greater than the sum of all the other *Spartina* areas of the harbor.

Starting at the northwest corner of the harbor, we find that there is a pocket in the shore about 200 feet in diameter quite filled with *Spartina,* except for a few tide-pools and a fresh-water stream from a ram. From this region eastward to 200 east the border of *Spartina* is 50 to 100 feet wide (plate VII A). It then suddenly broadens out until, from 500 to 900 east, the *Spartina* stretches out 600 or 800 feet southward from the shore of the Spit proper (plate I). This broad band of *S. glabra* along the eastern third of the Spit serves, we shall see, as a protecting barrier of great importance to the plants of the upper levels of the beach, above 6.5 feet.

From 800 west to 200 east the lowermost stands of *Spartina* are on bottom at from 2 feet to 2.5 or 3 feet above mean low water. Eastward from here the lowest or southernmost boundary of the *Spartina* corresponds pretty closely with the 1.5-foot tide-line or contour, as it does elsewhere about the harbor (see plate I). It is noteworthy that though the lower border of this marsh is very irregular as far as 600 east, from there eastward and northward it is quite regular. This latter fact is probably related in some way to the presence of the strong tidal-currents through the Inlet. We shall have occasion to recur to this later. The level of the soil bearing most of the *Spartina* for 30 or 40 feet inward from this southern margin of the Marsh lies between the 2 and 3 foot levels. The upper limit of *Spartina* throughout this band is near the 6.5-foot level (plate X). Only in a few places does it fall to, or slightly below, the 6-foot level, as on hard gravel or on shifting sandy bottom at 2,800 north by 900 east. In the northwest corner of the harbor, 900 to 1,000 west, rather thickly scattered *Spartina* may grow as high up as the 7.5-foot tide-line, though the dense, pure stand ends here as elsewhere at about 6.5 feet. The cause for a local rise in the upper limit at this point is perhaps to be found in the extreme flatness of the shore here, which causes poor drainage, such as we shall find on the marsh at the south end of the harbor. Possibly the wet soil here is due to the presence of fresh water in the subsoil, though no adequate evidence of this has been found. We do not find here *Scirpus americanus* or *S. robustus,* which are commonly found in soil containing fresh water at these levels.

The substratum upon which most of the *Spartina glabra* of this south shore of the Spit is growing is a more or less firm, peat-like muck. At the eastern end of the Spit, at both upper and lower limits, *Spartina* is found on a sandy bottom. The muck referred to may, at the upper end of the *Spartina* belt, be but a few centimeters in depth, while at the middle or lower portion of this belt there may be 0.5 meter or more of this muck, overlying the hard sand

or gravel. For example, a series of soundings through the mud of the bottom, at different levels, along the main north-and-south axis, beginning at 2,700 north, showed the following thicknesses of soft mud above the hard bottom: at the 6.5-foot level 5 cm. of mud; at the 6-foot level, 15 cm.; at the 5-foot level, 38 cm.; at the 4.5-foot level, 40 cm.; at the 4-foot level, 43 cm.; at the 3-foot level, 70 cm.; at 2.5-foot level, 66 cm.; at the 2-foot level, 36 cm.; finally, at the 1-foot level there was a thickness of but 30 cm. of mud above the firm subsoil. The thickness of the *Spartina*-bearing mud can be seen in the cross-section of this part of the shore of the harbor shown in figure 1.

The rhizomes of the *Spartina* branch freely and run along more or less horizontally at about 1 to 1.5 dm. below the surface of the mud. The rhizomes are about 7 to 9 mm. in diameter and the living portion is about 2 or 3 dm. long. It consists of several or of many internodes, and may branch several times in its length. The terminal bud of the main axis maintains its horizontal position, while the lateral offshoots turn upward and give rise to the aerial shoots. From the base of each of these shoots a new rhizome puts out, in the season after the leafy shoot is unfolded. By the network of interwoven rhizomes

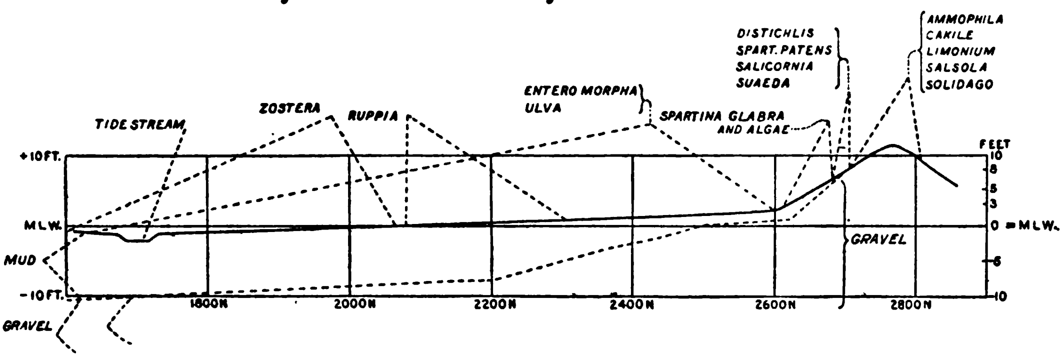

FIG. 1.—North to south vertical section, at 0 east, of the Spit and adjoining portion of bottom, showing the depth of peat or mud overlying the gravel substratum, and the more important plants that dominate each level. Horizontal scale 1 = 3,000. Vertical scale 1 = 300.

thus formed, which is in some places 4 or 5 layers thick, and by the roots which penetrate to still greater depths, the soft mud is firmly bound together for 2 or 3 dm. below the surface.

The aerial shoots push up above this substratum in the summer to a height varying from 1 to 2 meters, and sometimes have a diameter of 1.5 or 2 cm. at the base. In the denser stands of this grass there may be from 300 to 600 stalks per square meter. Each aerial shoot may bear 1 or rarely 2 bladeless leaves at its base and 6 to 12 complete leaves toward the top. The size and general vigor of the plants differ greatly with the level of the soil in which they are rooted, and is usually greatest on bottom between the 3-foot and 6-foot levels. For example, *Spartina* growing on mud between the 3 and 3.5 foot levels, near 2,200 north by 600 east, is 15 to 20 dm. high, while other plants nearby, on soil at the 1.5 or 2 foot levels, reach only 8 or 10 dm. in height.

The flowers of some of the *Spartina* plants begin to open in the latter half of July, nearly 3 months after the shoots push up from the stubble in late April, but it is only the more vigorous plants, *e. g.*, those on bottom between the 3 and 6 foot levels, that begin to bloom as early as this. The smaller plants at lower and

higher levels do not begin to bloom until much later than this, often in late August or even in early September. Apparently seeds are set rather freely on the stronger plants and a considerable crop of seedlings might be expected. As a matter of fact, seedlings are not very abundant, because, it seems, unoccupied soil of the proper character and at the proper levels is not frequent. The seedlings that have been found in midsummer were growing on bottom just above the 1.5-foot level, that had evidently been disturbed by clam diggers (100 north by 475 east), or by water-currents (2,000 north by 1,100 east and at mouths of Creek and rivulets), just at the time that the seeds were being dispersed by the water. This stirring of the bottom formed pits and furrows in which the seeds were readily buried.[a] Seedlings found at the first station mentioned, on July 1, 1911, presumably from seeds ripened in 1910, were from 1 to 2 dm. high, had leaves, and a well-developed root-system, though the glumes were still attached. Our search for seedlings more than a year old was unsuccessful. All medium-sized plants examined proved to be young shoots at the tips of long runners from mature rhizomes.

It is evident that the usual means of propagation and spreading to contiguous areas is by the longer branches of the rhizome. In this way the borders of a clump of *Spartina* may be spread 4 or 5 dm. in a year, but it probably takes several years to produce, on such an added area, a dense stand, such as was mentioned above, of 300 to 600 stalks to the square meter. Another means of spreading to more distant parts of the harbor is through transportation of whole tufts or mats of rhizomes by the ice. The stubble, which is tough in early winter, may apparently be frozen in blocks of ice at low tide, and when these blocks float up with the rising tide whole clumps of *Spartina,* with 2 or 3 dm. thickness of mud tangled among its rhizomes, may be lifted and carried to other parts of the harbor. It is only when these clumps happen to be dropped on bottom at or above the 1.5-foot level that they persist for more than one season. It might be assumed that clumps lodging below the 1.5-foot level disappear in winter through the agency of ice, but, as a matter of fact, they do not thrive even for one growing season. Dead clumps of turf are often seen on the bottom, showing where living turfs have been dropped. Early each summer one or more considerable clumps of the grass are found growing in new locations, sometimes near the very middle of the harbor. The death of this grass at levels below 1 foot or even 1.5 feet is probably due to its inability to withstand so long a submergence as it is there subjected to. Experimental work is under way by which we hope to determine whether this is the real explanation.

A very interesting feature of the distribution of *S. glabra* at its lower limit is the suddenness with which it ceases to spread downward over the bottom when the 1.5-foot level is reached (plate III A). The soil may be quite densely covered with *Spartina* even at the lower limit of its distribution, and the presence of its rhizomes gives the bottom sufficient firmness to enable it to support the weight of a person walking over it. The bottom just beyond that bearing *Spartina* drops abruptly to a level 6 or 8 inches lower. This lower bottom is usually very soft for a depth of several decimeters. About tide-pools and the little inlets making into the mid-littoral marsh, near 2,500 north by 200 east, we find this same sudden drop to lower and softer bottom. It is difficult to see why the

[a] Once only (at 100 north by 1,000 east) were seedlings of *S. glabra* found growing in the peaty mud among the parent plants near the 6-foot level.

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rhizomes of the reed-grass do not rather quickly occupy these areas, which might then soon be built up by the deposit of the silt brought in abundantly by the tide. The only plausible explanation of the persistent absence of *Spartina* below the 1.5-foot level is that the conditions encountered by the rhizomes or shoots at these lower levels are unendurable. Just what the ultimate injurious factors in these conditions may be we shall suggest later, in our general discussion of the factors affecting the whole distribution of *Spartina glabra*.

Practically the whole of the area south of the Spit, shown within the finely zigzag line on the chart, and up to just beyond the 6-foot contour, is covered continuously and year after year with *Spartina glabra*. The only considerable tide-pools and larger notches of bare mud along the margin are shown on our map. Moreover, aside from the relatively inconspicuous algæ matted about the stalks of the *Spartina,* where it is less dense in growth, no other plants participate with *Spartina* in occupying the soil. Absolutely no other established seed plants are found in this area until we reach the 6-foot level, where we begin to encounter inwandering angiosperms from the next higher belt of vegetation. A description of the species competing with *Spartina* at its upper limit, and also of the local distribution of *Spartina* itself at these higher levels, may be left until we take up the discussion of the next higher belt of vegetation.

On the east side of the harbor, because of the wharves, we find only one rather short strip of well-developed *Spartina* association. This one piece of natural shore on the east side extends from 100 south to 500 north, and the *Spartina* association is developed in a very interesting way here, evidently because of the presence of an abundance of fresh water along this shore. North of the mill, from 600 to 800 north, between 975 and 1,175 north, near 1,400 north, 1,650 north, 2,150 north, and 2,400 north, there are found strips of *Spartina* from 1 to 10 meters in width growing at 2 to 4 feet above mean low water, along the base of the wall of the wharves. These strips are covered by typical *Spartina* alone, except for the algæ usually associated with it, and will therefore not be considered further.

The *Spartina* belt between 200 north and 500 north forms a nearly continuous fringe, 10 to 30 meters wide, occupying the eastern shore between the 1.5 and 6.5 foot levels, though these limits vary slightly. From 200 north to 100 south the fringe of *Spartina* is only 10 to 15 meters wide, and is broken through at half a dozen points by fresh-water rivulets. The stand of *Spartina* shows much the same density and other characters here as on the Spit. The extreme lower plants, from 200 north to 500 north, are on soil at the 1.5-foot level, and are small and late in flowering. South of this the lower limit for this species moves upward till from 0 to 100 south the lowermost plants are often at 3 feet or even 4 or 4.5 feet above mean low water. The salt reed-grass is evidently kept up on high levels here by the high level of the neighboring tide-stream at low water. If, for example, at 100 south, *Spartina* were to grow at the 3-foot level, it must needs grow in the bed of the tide-stream, where the rhizomes would not only be submerged most of the time during low tide, but would also have to push through a firm gravelly soil. The eastern bank of the tide-stream all along here usually drops from a level that varies from 3 to 6 feet above mean low water, downward abruptly for 1, 2, or 3 feet to the stream-bed, and *Spartina* is confined to the top of the bank, or to undermined

portions of the *Spartina* turf that are hanging down into the stream. Along all the fresh-water rivulets shown on the map between 0 and 200 north the *Spartina* keeps upon the firm peat at the side, 6 or 8 inches above the constantly flooded gravel bottom of the rivulet. The rhizomes and roots must often reach down nearly to the fresh-water level. Only at one place about the harbor has *S. glabra* been found growing where its rhizomes are constantly immersed. This was in a pool of 10 feet in diameter filled by fresh water falling from the flume south of the mill (plate IV B). The surface of this pool was at the 5-foot level, and the *Spartina* is rooted in soil some inches below this, so that its roots and rhizomes were surrounded by fresh water for 6 or 7 hours each tide. In 1910 the water was shut off from this millrace and it is now dry. The only seed plant growing in the beds of these fresh-water rivulets is *Lilæopsis lineata,* which we have already mentioned as the only other seed plant characteristic of the *Spartina* belt. In the bed of one of these rivulets near 150 north, between the 4 and 6 foot levels, hundreds of these tiny plants with their bladeless leaves lie appressed to the gravel, while the cold fresh water runs over them for 6 to 9 hours each tide.

The steepness of the shore, the character of the soil, and the abundance of the supply of fresh water are very different on different parts of this eastern side of the harbor. In evident consequence of this we find that the upper limits reached by *Spartina glabra,* and by the other plants with which it comes into competition on the upper portions of the mid-littoral belt, are much more variable than on the Spit, where we found a very regular upper margin of the dense *Spartina* running along the 6.5-foot tide-line. For example, at 200 north there is a rather well-drained bit of mid-littoral beach. In this region the pure dense growth of *Spartina* ceases at the 5.5-foot level. At the 6-foot level it becomes rather equally mixed with *S. patens,* which becomes dominant from this level up to 7.5 feet. Only a few scattered small plants of *S. glabra* reach to the 6.5 and 7-foot levels. At 350 north, where the east shore between 5 and 7.5 feet is of coarse gravel, and supplied with very little fresh water trickling over the beach at low tide, the pure stand of *S. glabra* ends at 5.5 feet, where it becomes mixed with *Scirpus americana* and with still fewer plants of *Spartina patens.* Above the 6-foot level the latter becomes dominant and *S. glabra* is sprinkled more and more sparsely with it, and with *Scirpus americanus,* up to the 7-foot level. Above this the *S. glabra* is wanting altogether.

From 400 to 500 north, where, in some places fresh water is trickling over the beach from above the 8-foot level, and in other places where it is seeping out of the gravel at lower levels, we find the dense *S. glabra* going up to the 6.5-foot level, in places where the turfs are kept continually moist by fresh water running constantly about them. Here, as elsewhere, it does not grow at all where fresh water is running directly over the soil in which its rhizomes are embedded. Usually this is evidently because the fresh-water rivulet cuts away the peaty soil down to the underlying gravel in forming its little channel. The rhizomes, except in the pool below the mill-wheel, are always in soil high enough above the beds of these rivulets so that the soil-water always remains more or less saline even at low tide. It is probable also that the water constantly running over the beach may keep the air about the leaves of the short *Spartina* of the upper levels more than usually moist during low tide and thus, by reducing transpiration, enable it to creep a little higher up the beach. Along

most of this shore from 350 to 500 north the *Spartina* is not replaced at its upper margin by a dense growth of *Spartina patens,* as it generally is further south, but instead by a relatively bare gravelly beach merely sprinkled with plants, which are, however, of considerable variety. Thus, for example, plants of *Solidago sempervirens* are encountered at 6 feet, and a few seedlings even at 5 feet. *Salicornia europæa* is found from the 5-foot to the 6-foot level. *Atriplex patula hastata* occurs at 5.5 feet, out of reach of fresh water. *Scirpus americanus* follows the fresh water down to 6 feet. *Triglochin maritima* goes down to 6 feet. *Plantago decipiens* first appears at 6.25 feet. *Scirpus nanus* forms dense turfs on mud out of reach of flowing fresh water at the 6.25 to 6.75 foot levels. These plants apparently are able to invade the *Spartina* belt because the presence of fresh water, either by its direct action on the roots or by washing away the peat from above the gravel, makes it difficult or impossible for the *Spartina* to compete with the invaders on these areas. Most of these competitors, it should be noted, are established on the bare gravelly areas. Only the *Scirpus americanus* and *S. nanus* and some plants of *Salicornia* and *Plantago* are found on mud, the favorite soil of the *Spartina.*

The western shore of the harbor is not so completely occupied by wharves as is the eastern, and it therefore bears much larger strips of *Spartina glabra.* From 550 to 1,050 north the fringe of *Spartina* varies from 12 to 20 meters in width and has quite regular upper and lower borders, the former being throughout very close to the 6.5-foot level, and the latter running along between the 1.5 and 2 foot levels. From 1,220 to 2,400 north the *Spartina* belt is much more irregular in distribution, probably because of local differences in the amount of shade and of fresh water present along this part of the shore. The width of the *Spartina* association varies from 5 or 6 to 30 or 40 meters, as may be seen on the chart, and it is interrupted only by the fresh-water streamlets and by a small wharf at 2,200 north. The lower margin of the stand of *Spartina* runs along at or just above the 1.5-foot level as far as 2,000 north, but in the extreme northwest corner of the harbor retreats to the 2.5 or even to the 3-foot level. The upper margin runs near the 6.5-foot contour, but in a few wet or shady areas fairly dense growths of *Spartina* have been found at 7 or 7.5 feet, and scattered plants at even the 8-foot level.

The stand of *Spartina* along the west shore, except where it extends above the 6.5-foot level, is pure and generally very dense. There are often 500 or 600 stalks per square meter. The plants vary from a height of 6 to 9 dm. in the upper parts of the belt to a height of 18 or 20 in the middle and from 6 to 10 or 12 near the lower margin. The largest plants seen were 23 dm. high. These were growing in a layer of mud 1 dm. thick, overlying a sandy subsoil at the 3.25-foot tide-level. On most portions of the west shore the bottom rises with a very sharp slope from about the 4-foot to about the 6-foot level. The plants of *Spartina* are all within a strip a few meters in horizontal width. Those plants growing on levels below 4 feet are rather short, being from 8 to 10 or 12 dm. high, while those growing between 5 and 6 feet are commonly 15 to 18 dm. high. The difference in level of bottom, combined with difference of size of plants, makes the *Spartina* appear, to one rowing along this shore when the tide is nearly low, as though it grew from two terraces of 3 or 4 feet difference in level. At half tide the outer edge of the *Spartina* on the upper terrace rises so abruptly above the water that it appears to be the outer margin of the whole *Spartina* belt.

The blooming of the *Spartina* on the west shore shows the same features that have been noted in plants growing on the Spit.

The largest areas within the boundaries of this part of the *Spartina* belt that are not covered more or less densely by this grass are the beds of the fresh-water streams entering the harbor on the west side. The more important of these are indicated on the map. Wherever any considerable rivulet runs down over the beach it cuts the *Spartina* belt clear across by washing off the peaty mud down to the underlying gravel. The smaller of these channels, running across the beach, are but a decimeter or two in width, while the larger ones may bare the gravel for a width of 1, 2, or rarely 3 meters. On the edges of these channels the firm mud, on which the *Spartina* grows, stands at a level of 2 to 4 dm. above the bed of the rivulet. On the edges of these steep banks the *Spartina* stops abruptly, just as we have seen it do along the tide-stream in the southeast corner of the harbor. This is also much the way the stand of *Spartina* ends about the reentrant notches along its ragged outer border. Such notches are found especially along the west shore. On the projecting points of the dissected edge of the *Spartina* area, however, the firm peat slopes off gradually to the soft mud of the harbor bottom, and here the *Spartina* does not stop abruptly, but thins out rather gradually. Much of the raggedness of the outer edge of the *Spartina* belt is probably due to the burrowing through the substratum of the muskrat (*Fiber zibethicus*).

The stand of *Spartina* along the west shore is practically pure up to the 6-foot level. The only other plants commonly occupying the bottom between these levels are the gelatinous or felted green and blue-green algæ, with occasional tufts of *Ascophyllum* and tangles of *Fucus*. On two small areas close together at 1,845 north and 1,860 north a few hundred plants of *Lilæopsis* were found between the 6 and 6.5 foot levels (plates XII and XXII). As in the case of the *Lilæopsis* found in the southeast corner of the harbor, these also seem to be associated with fresh water. In these particular areas on the west shore there is no fresh water running over the surface, but if a stake is pushed into the soft, spongy mud and withdrawn, the water collecting in the hole is entirely fresh to the taste. Moreover, there is fresh water seeping out to the surface 3 or 4 meters down the beach, and forming a tiny rivulet from the 5-foot level downward. The only place about the harbor where *Lilæopsis* is not evidently associated with fresh water is at 60 north by 1,050 east, where, however, it is just beside the tide-stream, the water of which is only brackish, at the surface, at the time it covers the area in question.

On the west shore, as on the east side, the upper boundary of the pure growth of *Spartina glabra* is less regular where the beach is shaded or saturated with fresh water. The plants succeeding the *Spartina* at its upper limit are different as these conditions differ. The three species with which *Spartina* is most often mingled at its upper margin, and by which it is displaced slightly higher up, are *Spartina patens*, *Distichlis spicata*, and *Scirpus americanus*.

In regions where the beach is gently sloping, and well drained between the 6 and 8 foot levels, *S. glabra* is usually succeeded by *S. patens* or *Distichlis*, and commonly these are mixed. The distribution of the areas occupied by these smaller grasses will be given in detail in discussing the next higher belt. We will simply cite examples here to indicate conditions found at the tension-zone. At 1,660 to 1,700 north, for example, *S. glabra* meets *S. patens* at the 6.5-foot

level, and with very little intermingling the *S. patens* becomes as completely dominant a meter or two above (*i. e.,* inshore from) the meeting-line as *S. glabra* is a meter or two below the line. Mixed with the *S. patens,* a little higher up are scattered plants of *Distichlis,* and, in the wetter portions, of *Scirpus americanus.* A few dwarfed, scattered shoots of *S. glabra* are found even as far up as 7 or 7.5 feet. On the well-drained areas the tension-zone between the *Spartina glabra* and the *S. patens* is much narrower and the last scattered stalks of the *S. glabra* get very little above the 6.5-foot level (*e. g.,* at 840 to 900 north). It seems clear that elevation of the soil is the condition favoring the success of *S. patens* in the competition. Thus, for example, at 1,760 north there is a complete island of *S. patens* on soil at 7.25 to 7.5 feet, surrounded entirely by *S. glabra* on soil running up to about the 7-foot level, the zone of the latter on the upshore side being 1.5 meters wide. The elevation of this patch of soil above its immediate surroundings on all sides, with the better drainage thus allowed, was the only discoverable cause of the difference in its vegetation.

On parts of the west shore where fresh water is abundant *S. glabra* encounters *Scirpus americanus* at its upper margin. It is in these areas that we find the most interesting and diverse behavior of the salt reed-grass and its competitor. Each is dependent upon the character of the soil, its fresh-water content, and the amount of shade to which it is subjected. In general, these two species, when growing on wet shores, mingle much more freely and widely than do *S. glabra* and *S. patens.* For example, at 1,220 north *S. glabra* nearly 2 meters tall becomes mixed with *Scirpus americanus* at the 6-foot level, and then continues on upward to the 7.25-foot level. The *Scirpus* occurs here on soil between the 6 and 8 foot levels that is more or less covered by fresh water at low tide, while the *Spartina* is found as usual on soil above the level of running fresh water. At other points nearby (1,325 north), where the fresh water, though evidently present in the soil at higher levels, does not break out as a rivulet till the 5 or 4 foot level is reached, *Scirpus* gets down to the 5-foot level on higher lumps of peat. In this area the *Spartina* ceases at the 6.25-foot level, with plants of 6 or 7 dm. in height. At 1,700 north the *Spartina* meets the *Scirpus* at 6.5 feet, where the latter immediately becomes dominant and continues up to the 8-foot level, with only the barest sprinkling of dwarfed *Spartina* plants between 6.5 and 7 feet. In general, then, where fresh water is present on an unshaded shore, the *Spartina glabra* becomes mixed with *Scirpus americanus* from 6 feet upward. In regions that are both wet and moderately shaded we have a very interesting change in the relative distribution of these two species. Under these conditions the *Scirpus* is mixed abundantly with the *Spartina* from 6 to 6.5 or 7 feet and then ceases, while the *Spartina* becomes more abundant again and continues upward in moderate shade to 7.5 or even to 8 feet (*e. g.,* at 740 north and near 1,350 and 1,400 north). The relation of the two plants at these points seems to show that the *Scirpus americanus* cannot endure much shade; that *Spartina glabra* can endure moderate shade, as indeed it must when submerged; that *Spartina* pushes up the beach far beyond its competitor *Scirpus* in shaded areas where fresh water is present, and where, therefore, the moisture content of the air about the leaves is sufficient to prevent a too rapid transpiration.

The other angiosperms which may mingle with *Spartina glabra* along its upper margin on the west shore are, in order of abundance, *Solidago sempervirens, Atriplex patula,* and *Scirpus robustus.* Of these, *Solidago* and *Atriplex* occasionally mingle with *Spartina glabra* near the 6.5-foot level (*e. g.,* 1,250 north), but they are usually encountered by the *Spartina* only when it has pushed farther up the beach. This is true also of *Scirpus.* None of them except *Scirpus robustus* (at one or two spots) is an important competitor of *Spartina,* and further discussion of their distribution may be left until we take up that of the plants of the next higher belt.

The mid-littoral *Spartina* belt on the Marsh at the head or south end of the harbor is more largely developed than on any other part of the shore except on the eastern half of the Spit. Aside from the greater variety of competitors met at some points along its upper margin the general character of this broad belt of *Spartina glabra* is similar to that on the Spit.

Since a special study has been made of the successive levels of the whole Marsh at the head of the harbor (mid-littoral, upper littoral, and supra-littoral marshes), and Professor Conard has mapped in detail the vegetation of a selected strip, cutting across all three of these belts (see plates XI, XXI, and XXII), we will here only sketch the most general features of this portion of the mid-littoral belt. It will be noticed at once on plate XI that the main stream cuts into halves the whole marshy area south of the harbor, from the 1.5-foot level up to the 9-foot level. The portion on the west of the stream is chiefly below the 6.5-foot level and therefore largely occupied by *Spartina glabra.* That east of the stream lies chiefly above the 6.5-foot level and therefore has a relatively narrow belt of *Spartina* at the north and a bare fringe along the stream. The lower limit of the *Spartina* across the whole northern border of this belt, from 200 east to 1,000 east, is between the 1.5-foot and 2-foot levels, a little higher on the average than on the east end of the Spit and than on the more open portions of the east and west shores of the harbor. The stand on the south shore is rather thinner at the edge, but soon attains a density comparable with that on the Spit, and increases also in size as it goes up to higher bottom (indicated in the section of soil and vegetation, figure 3). On each side of the large stream, a shoal, coming just above the 1.5-foot level, begins at 50 north and stretches northward toward the harbor. The shoal on the west side is being steadily taken possession of by *Spartina glabra,* which, during the six years our investigations have covered, has advanced several meters. Comparison of the present northern limit of the *Spartina* in this locality with that shown on a map made in 1902, by Shreve, indicates that it has pushed northward 12 meters in 10 years. The shoal at the east of the stream is not being occupied by the *Spartina,* probably because the corner of the *Spartina* belt at 75 north by 650 east is held back by an artificial bathing-beach across the south end of the shoal, which is cleaned off each year. The irregularities in outline of the *Spartina* belt west of the stream, especially in the deep notch at 400 east, are apparently connected with the entrance of a stream that is dry in summer but in winter and spring carries considerable fresh water into the harbor.

Along the Creek and the tide-stream at 1,000 east the character of the lower margin of the *Spartina* belt differs on different parts of the stream-bank. Having incidentally referred to the conditions along the tide-stream when discussing the *Spartina* of the east shore, we will here discuss conditions only along

the Creek. In general we find on the concave side of each bend a steep bank (plate XV B), formed by the caving of the firm turf of *S. glabra* and *S. patens* from the edge of the Marsh, as the soft material below is cut out by the stream. For example, at 100 south to 200 south on the east bank large blocks of the Marsh soil, 3 or 4 meters long and a meter thick, are often cracked off. These blocks either settle down while keeping the *Spartina* turf in a horizontal position, or become tilted over by the rapid undermining of the western side, until the turf stands nearly vertical. In the substratum, with the root-collar 3 feet or more below the present Marsh surface, stumps of *Acer rubrum* are found *in situ*. The top of the Marsh along this bank, from 0 to 200 south, rises to the 7-foot level only 2 or 3 meters back from the edge. From this level it slopes down quite rapidly to a level of 6 feet or somewhat less at the very margin, evidently because of the settling of the surface, as the soft peaty mud below it is washed away or squeezed out toward the stream. It is only this narrow, sloping brim that is occupied at all completely by *Spartina glabra*. The stand is often quite sparse, apparently because the bank caves and the soil settles more rapidly than the *Spartina* can completely occupy the new areas thus brought down to the proper level for it. The denser stand of *Spartina* here often ends quite abruptly in some places, so that beyond 0.5 meter from the upper or on-shore limit of dense *Spartina* not more than half a dozen isolated plants of this grass can be found for 5 meters along the bank. On this eastern bank, from 200 south to 500 south, where the bank is not being undermined, it slopes much more gradually, and the *Spartina* belt is wider. (See plate XI.)

The western bank of the Creek, except from 350 south to 450 south, is a convex one. In consequence, we have an abrupt bank, with the *Spartina* belt very narrow, only in the particular region just specified, where the conditions are like those of the east side between 0 and 200 south. From 300 south to 200 north the west bank is a gently sloping one with a very wide belt of *Spartina*. The stand of *Spartina* on this west side shows a range in density and height like that on the Spit and on north edge of the Marsh. It is practically continuous, except where cut through by branches of the main stream and smaller side streams, or where it is temporarily killed out by flood-trash. As an example of the latter we may cite an area about 6 by 12 meters at 430 south by 720 east which was covered by flood-trash during spring and summer in 1911. In September 1911 not a green shoot of *Spartina* could be seen on this area, though elsewhere this grass was still fresh and green. These areas, when the trash is floated off again, become covered first with algæ, as we shall soon see, and only gradually are they reconquered by *Spartina*, through the growing inward of rhizomes from the *Spartina* plants round about.[a]

The upper margin of the *Spartina* belt here at the head of the harbor lies between the 6 and 7 foot levels. The map shows that the margin is generally quite regular, except for the tongue pushing upward along each stream. A sudden ending of the dense stand occurs rather frequently at the upper margin of its belt along the north shore of the Marsh (700 to 1,000 east). In some places on this shore the bottom rises rather abruptly from the 6-foot to the

[a] In the summer of 1913 a patch of *S. glabra* 40 square feet in area (at 200 north by 1,000 east) was smothered out by masses of *Ulva*. When the latter was washed off by storm tides the dead leaves and culms of the grass were quickly felted over by *Lyngbyas*, *Oscillatorias* and *Microcoleus*.

7-foot level, all in a horizontal distance of 0.5 or 1 meter. The *Spartina* at the foot and part way up this slope is quite dense. On the upper half of the slope it thins out, and when the top of the slope is reached at 6.75 or 7 feet it is replaced by its commonest successor, *Spartina patens,* except for a bare sprinkling of small shoots of the *S. glabra* in areas with wetter soil. Where, however, there are tide-pools farther up on the Marsh, the *S. glabra* extends back along the edges of the draining ditches and often occupies not only the sides but sometimes the bottom of the pool itself, though this may lie above the 7.5-foot level (*e. g.,* the tide-pool at 100 south by 900 east). Other areas, with a firm bottom, that lie but a few inches below the surface of the surrounding Marsh, and have no outlet on the surface, may bear small plants of *S. glabra* in rather dense stand—100 or 200 plants per square meter. Such an area is found at 0 north by 1,025 east (plate XI) and another very interesting one just above the 8-foot level at 240 south by 1,135 east, as is indicated in plate XI, area 25. (See C. A. Davis, 1910.)

Along the portion of the shore from 100 south by 400 east to 250 south by 600 east, the upper margin of the *Spartina* belt much resembles that of the Spit. The soil here is sandy, and at the 6 to 6.5 foot levels *S. glabra* meets and mingles with *S. patens* and more rarely with *Distichlis.* It also comes in contact occasionally with scattered plants, but never with dense stands, of *Solidago sempervirens, Salicornia europæa,* and *Spergularia.* Near the fresh-water rivulet at 320 south by 640 east the *Spartina* encounters and mingles with *Scirpus americanus,* which also occurs on both sides of the main stream beyond 400 south. The related species, *S. robustus,* is mingled with the *Spartina* between the 6.5 and 7 foot levels at several points where the soil is considerably saturated with fresh water (460 south by 820 east, 100 south by 1,180 east).

Some details of the distribution of these competitors of *Spartina* and also of certain rarer ones are indicated in plate XI.

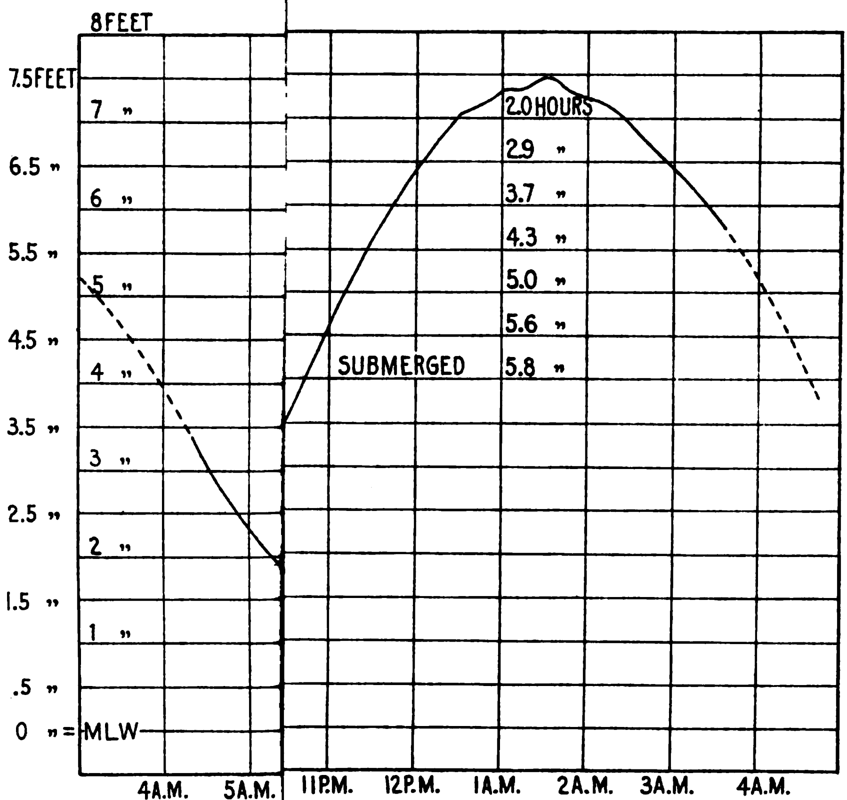
Throughout this *Spartina* belt about the south end of the harbor, aside from the competitors very near the upper margin, no other seed plants are found, except the small patches of *Lilæopsis* (60 north by 1,050 east and 150 north by 1,140 east), which grow on bottom between the 5 and 6.5 foot levels. Dr. Shreve records the occurrence of *Limosella aquatica* var. *tenuifolia* on the edge of the shoal near 199 north by 600 east, but this has not been seen in recent years.

Most of the algæ found scattered among the *Spartina* on the other shores are equally abundant here, and will be referred to again in a later section.

THE FACTORS DETERMINING THE DISTRIBUTION OF SPARTINA GLABRA.

Having sketched in some detail the distribution of this salt reed-grass about the whole harbor, and described the habitats in which it grows, we may now attempt to discover the enviromental factors that condition the distribution which we actually find. What factors have favored the entrance and persistence of the grass in the areas now occupied, and what factors limit its extension upward, downward, and horizontally along the shore? We should keep in mind that many of these factors probably act in a similar way on other plants, and that for this reason *Spartina* is a type whose relation to external factors is in many respects resembled by that of many other plants about the harbor.

Temperature and light of the range of intensities found, so far as has been made out, play no decisive part in limiting the distribution of *S. glabra.* It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SUBMERGED
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5 A.M.
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2 A.M.
3 A.M.
4 A.M.

A. South Shore of Spit looking West from 200 West, showing Cross-section of Belt of *Spartina glabra*, left by Mowing. The 3 Stakes with Placards are (left to right) at the 4-foot, 5-foot, and 6-foot Levels respectively.

B. South Shore of Spit, near East End, showing Zonation between 6 and 10 feet. In foreground *Suæda*, *Limonium*, *Spartina patens*; at left *Solidago* and *Ammophila*. The Numbered Stakes are set at the indicated Tide Levels on Beach.

seems to grow equally well on warm tidal flats, or where flooded by the cold water of tidal inlets or fresh-water streams. It is possible that it is the low temperature of the spring-water of the rivulets along the east and west shores that prevents the *Spartina* from gradually invading the beds of these streams. In certain areas along the west shore it endures considerable shade, though it commonly grows in full sunlight. These shaded plants, however, are at high levels and hence they enjoy, from the neighboring trees, about the same degree of protection from light and transpiration that plants at lower levels do from submergence.

The character of the soil is evidently a factor of much importance near the upper and lower limits of the *Spartina's* distribution. Between the 2-foot and 6-foot levels *Spartina* may grow on mud, peat, sand, or gravel, as may be seen along the Spit. It has been pointed out, however, that the belt of this grass stops most abruptly at its upper margin on a gravel beach, just east of the middle of the Spit. At its lower margin, in like manner, the *Spartina* usually terminates abruptly at a point where the very soft mud succeeds the rather firm peat. This is equally true whether the change in character of the soil occurs at the 1.5-foot, the 2-foot, the 3-foot, or even at a higher level, as it does in the northwest corner of the harbor and about certain tide-pools.

From these facts we might conclude that this plant is gradually advancing over the soft bottom and binding it together with its roots and rhizomes. But on this assumption it is rather surprising to find such a very regular lower limit of distribution at the 1.5-foot level in a harbor where this grass has been growing for hundreds of years. It will also be difficult to explain the greater width of the *Spartina* belt at the east end of the Spit. On the whole it seems clear that the firm soil bearing *Spartina* is in some way the product of the growth of this grass and that it is the conditions limiting the spread of *Spartina* that secondarily determine the extent of this firmer bottom.

All observations thus far made on this harbor indicate that the decisive factors preventing the *Spartina* from spreading further upward or downward are those connected, directly or indirectly, with the water-level about the leaves or in the soil about the roots. In short, the primary factors may be considered under two heads—tide-levels and fresh-water streams or springs.

TIDE-LEVELS.

Differences in the elevation of soil above mean low water may, in the first place, influence the distribution of *Spartina* directly by determining the time of submergence. Upon this depends the level maintained by the salt water in the soil about the roots of the grass and the time of exposure of the leaves to the evaporating influence of the air. These differences of level, and so of duration of submergence, may affect the distribution of *Spartina* indirectly, since the longer submergence evidently keeps the competitors of *Spartina* off the lower parts of the beach. The duration of submergence also determines the types of plants that grow just above the *Spartina* and thus the conditions in the soil into which the latter must push if it is to advance upwards.

At the lower margin of the *Spartina* belt at the east end of the Spit the soil at the 1.5-foot level is submerged for about 8.5 hours each tide, or for 17 hours daily, and exposed for only 7.5 or 8 hours daily. In certain areas remote from the main tidal currents, as in the northwest corner of the harbor, the

Spartina, as we have seen, retreats to the 2.5 or 3 foot level. It is believed that the long submergence affects the *Spartina* unfavorably by preventing the air from reaching the submerged rhizomes and roots. In the northwest corner of the harbor, out of the main currents, the water moves less, and hence the soil about the *Spartina* roots is less well aerated, and so this plant can not grow here at levels where it flourishes at the east end of the Spit, in better aerated soil, beneath the swifter tidal currents. It is also to be noted that crab and muskrat burrows are less abundant at the lower levels, and hence do not aid in aerating the soil.

The change of water-level, due to the tides, keeps the soil at the upper margin of the *Spartina* belt submerged for 2.5 to 3 hours and exposed for between 9 and 10 hours each tide. When covered this soil is probably nearly saturated. During emergence the water not only runs off the surface, but also settles out of at least the upper layers and, by way of the fiddler-crab and muskrat burrows, the air penetrates to the soil about the roots and rhizomes of the *Spartina.* The upper layers of the mud are firm enough to allow the fresh water of rains at low tide to run off so rapidly that little of it penetrates to the roots of plants.

The immediate effect of the semidiurnal change of water-level on the leaves and shoots of *S. glabra* is to expose it wholly to the air and the heat of the sun during low tide. This occurs for 17 or 18 hours per day for plants at the 6-foot level, for about 13 hours at the 4-foot level, and for only about 8 hours per day for those at the 2-foot level. The plants thus exposed show a distinctly xerophytic structure in their stiff and thick-cuticled leaves, which roll up tightly in drying winds. The evident usefulness of these xerophytic structures in plants growing at 6.5 feet and lower might suggest that *Spartina* is kept from invading levels above this limit because it can not endure the longer exposure of its shoots to desiccating winds and sun. But, on the other hand, we must remember that the *Spartina* growing at 5 or 6 feet is as large and vigorous as any plants of this species found, showing that there is no considerable reduction in size and vigor as this plant approaches its usual upper limit. Moreover, at high levels, in poorly drained soil, as, *e. g.,* on the west shore and on the Marsh south of the harbor, *Spartina* grows to a good size, although its leaves are always exposed to the air. But the surrounding air is in most of these cases rendered unusually moist by the presence of abundant water on the surface of the soil or by an abundance of neighboring vegetation.

All of these facts taken together seem to indicate that a low degree of saturation of the soil with salt or brackish water is a still more effective deterrent to the upward spread of the *Spartina* than the desiccation due to emergence above water-level.

INDIRECT EFFECTS.

It is clear that the direct effect of submergence or exposure in allowing or preventing the competitors of *Spartina* to grow at certain levels may indirectly affect, to a very marked degree, the distribution of *Spartina* itself. For example, the distribution of such plants as *Spartina patens, Distichlis, Salicornia,* and *Scirpus americanus,* which succeed the *Spartina* above the 6.5-foot level, indicates that these plants can endure neither as long submergence nor, perhaps, as high salinity of the soil water as *S. glabra.* We have already noted that *S. glabra* can grow up to levels as high as 7.5 or 8 feet, often mingled with *Spartina patens, Scirpus americanus,* and other plants. The most important

cause of the usual absence of *S. glabra* from the upper littoral region is, it seems clear, the competition of the plants above mentioned. Wherever the physical conditions allow these competitors to grow they prevent *S. glabra* from occupying levels higher than 6.5 feet. It is difficult in this, as in all cases of direct competition, to discover exactly how these plants of higher levels (*e. g., S. patens*) can prevent the advance of *S. glabra* into the areas occupied by them. If it is really these competitors that prevent the growth of *S. glabra* in certain areas, it must be by some effect exercised beneath the soil, since we can not believe that the shoots of the larger plant can be crowded or shaded out. It is possible that the dense impervious turf of *S. patens* cuts off the air from the deeper-growing rhizomes and roots of *S. glabra*. This would be in accord with the suggestion offered above, concerning the absence of *S. glabra* from poorly aerated mud of bottom below the 1.5-foot level. We are now attempting to solve this question experimentally.

Currents created by the rise and fall of the tides apparently have little effect on the distribution of *Spartina*, except that already noted of undermining the turf beside the two chief streams of the Marsh, and a similar, though relatively slight, effect along the tide-channel, cutting through the *Spartina* belt at the end of the Spit (near 800 east).

FRESH WATER IN THE SOIL.

In places where the fresh water runs over the soil the *S. glabra* is wanting. Often the peat is cut away down to the gravel by the flow of the rivulet. In other places the fresh water merely seeps out or trickles over the peaty mud. On this kind of area *Spartina* is sparse or wanting, and its competitor, *Scirpus americanus*, becomes more and more abundant as the soil becomes more nearly saturated with fresh water. Cases of this sort, of which there are many about the harbor, might seem to indicate that *S. glabra* can not grow in a soil saturated or nearly saturated with fresh water. But this *Spartina* does grow in the pool below the wheel of the old mill. The soil here at the time these observations were made was submerged in fresh water for 6 hours each tide, and could hardly become very strongly saline even at high water.[a] It therefore seems quite possible that the competition of the *Scirpus americanus* plays an important part in crowding *Spartina* out of areas wet by fresh water.

The usual intermingling of *Spartina* and *Scirpus americanus* in wet soils above the 6-foot level may quite possibly indicate that some individuals or strains of *Spartina* possess much greater ability to withstand fresh water than others and so push farther up the beach. Likewise, it may well be that the lowest plants of *Scirpus americanus* are really the individuals most able to endure salt water about both stems and roots. Only after experimental study of the problem can it be determined whether the position of the line of contact of these two species is dependent upon physical conditions directly or upon some kind of competition in which one plant disturbs the other physiologically. This study must include a determination of the power of different plants of the two species to endure considerable, and rapid, changes in the osmotic pressure of the water about roots and shoots.

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[a] A thin sprinkling of *S. glabra* grows south of the Causeway about 450 south and 800 east at the 7.5-foot level in soil water with a specific gravity of 1.000. Turfs of this grass planted in the pond 200 yards south of the Causeway survived but a single season.

The past history of this *Spartina* belt is indicated by stumps and other plant remains found in the peaty subsoil of the Marsh at the head of the harbor. It seems evident that the history of these *Spartina* marshes has been that outlined by C. A. Davis for the salt, tidal marshes near Boston, which have similar fresh-water deposits, stumps of trees, and other features like the marshes we are describing (see Davis, 1910, p. 635, *ff.*). The minimum amount of subsidence, as indicated by the plant remains found in the section of the Marsh on the east bank of the stream at 100 to 200 south, is about 6 feet. It is difficult to see how these remains can have attained their present relation to tide-levels by change in magnitude of the tides or by the settling of a floating bog, as held by D. W. Johnson (1913). We know of no evidence for the former change, and the fact that the salt-marsh peat does not overlie the parts of the gravelly shore (*e. g.*, near 100 to 300 south by 1,200 east) above the present marsh-level, seems to exclude the latter explanation.

2. The Algæ of the Mid-Littoral Marsh (1.5 to 6.5 Feet).

The number of species of algæ growing among the *Spartina*, on the natural shore lying between the 1.5 and 6.5 foot levels, is quite large. At least 36 species have been collected, and the distribution of most of these has been studied with some thoroughness. The classes and genera represented here, many of them by small patches or scattered individuals, are the following:

Schizomycetes: *Beggiatoa.*

Schizophyceæ: *Anabæna, Chroococcus, Lyngbya* (2 species), *Microcoleus* (2 species), *Oscillatoria* (3 species), *Polycystis, Rivularia,* and *Spirulina.*

Bacillariales: *Melosira, Pleurosigma,* and many less abundant species of other genera.

Chlorophyceæ: *Chætomorpha, Cladophora, Enteromorpha* (3 species), *Ilea, Monostroma, Rhizoclonium* (2 species), *Ulva,* and *Vaucheria.*

Phæophyceæ: *Ascophyllum, Ectocarpus, Fucus* (2 species), *Pylaiella,* and *Ralfsia.*

Rhodophyceæ: *Bostrychia, Delesseria, Hildenbrandia,* and *Petrocelis (?).*

Of all these species growing on the *Spartina* Marsh, the most prominent, because of their size, are *Ascophyllum* and *Fucus.* The most universally present are two species of *Rhizoclonium (R. riparium* and *R. tortuosum).* In some places these *Rhizocloniums* develop nearly pure growths of considerable extent, while in other habitats one or both species may form an important constituent, often the major one, of tangled mats, or, near the 6.5-foot level, of dense felts of algæ. These mats or tangles are mixtures of varying proportions of *Cladophora expansa, Enteromorpha clathrata,* and *Vaucheria thuretii?),* and often include also several or many species belonging to the genera *Calothrix, Lyngbya, Microcoleus,* and *Oscillatoria.* The closer felts or incrustations are more characteristic of the next higher belt and will be discussed in that connection. Below 6.5 feet it is only on the occasional spots bare of *Spartina* that these felts of algæ invade the present belt. They occur on the mud at the edge of the rivulets and between the stems of *Spartina,* and sometimes grow upon the stalks and stubble of this grass.

Keeping in mind the general constitution and distribution of these composite mixtures, we will now discuss the species of algæ occurring on this mid-littoral marsh in systematic sequence.

SCHIZOMYCETES.

Of the bacteria only one species is at all prominent in the thallophyte flora of the sublittoral belt. This is an undetermined species of *Beggiatoa,* which frequently forms stringy white coatings over the bottoms of the tiny rivulets of salt water which run off the marshes or out of the banks of the ditches and larger streams. It occurs between the 3-foot and 6-foot levels, always on bottom that is continually covered by the trickling water while the tide is low.

SCHIZOPHYCEÆ.

Of this group there are 12 species on the *Spartina* marsh and along the streams crossing it. The distribution will be described for each species in alphabetical sequence. (For distribution of important species see plate VIII.)

Anabæna torulosa: This is the most abundant and widely distributed of all the Schizophyceæ of this mid-littoral belt. Its nearly circular, gelatinous, glistening patches are from 1 to 10 cm. in diameter, and are found on the firm mud among the *Spartina* stalks between the 4 and 6 foot levels. The patches are very noticeable, as they have the appearance of huge greenish-black ink blots on the gray mud. These are chiefly *Anabæna,* but sometimes have a small admixture of *Lyngbya* sp. or of *Microcoleus.* In other places *Anabæna* forms a minor constituent of loose felts over dead leaves of *Spartina,* which consist primarily of *Lyngbya, Microcoleus,* and *Oscillatoria. Anabæna* is apparently a summer denizen of this belt. Its striking dark-green, gelatinous blots were entirely absent from their usual habitat in both April and September of 1911. The lowest level at which *Anabæna* has been found is 4 feet. The highest patches were seen among the stalks of *Scirpus americanus* at the 7-foot level. This alga seems to be most frequent near the fresh-water streams. For example, it is found along the edge of the large marsh south of the harbor and along the west shore, which, as we have seen, abounds in fresh rivulets and springs. It has not been found forming pure growths on the south shore of the Spit, where fresh water is wanting.

Chroococcus turgidus was found only occasionally, and then it was on erect stubble of *Spartina glabra* near the 6.33-foot level.

Isactis plana is a rather frequent constituent of the felts on the Marsh, being usually mingled with the *Lyngbyas, Vaucherias,* etc. (300 south by 625 east at 6 feet).

Lyngbya æstuarii, L. semiplena, and two or three unidentified species are of frequent occurrence in the present zone, between the 4-foot and 6.5-foot levels. Most, if not all, of these are also found above the limits of this belt. These species, when found in the present belt, usually grow on the mud about the bases of the *Spartina,* and form parts of mats or tangles, in which species of *Rhizoclonium* and its allies *Chætomorpha* and *Cladophora* are the chief constituents. This mixture is found very generally about the harbor, where there is sufficient light for the algæ between the *Spartina* stalks. It is especially frequent along the borders of the little rivulets of brackish fresh water that run across this belt from the upper beach. It is also seen among the *Spartina* where the latter is more scattered, at the upper margin of this mid-littoral belt. These same *Lyngbyas* are also found mixed rather sparsely with *Anabæna* near the 4 and 5-foot tide-levels.

Microcoleus chthonoplastes occurs in rope-like bundles more or less abundantly scattered through the mats of *Rhizoclonium, Lyngbya,* etc., just mentioned. It also occurs in nearly pure blackish-green gelatinous patches on the otherwise bare mud among *Spartina* stems between the 4-foot and 6.5-foot levels. It is found also in the next higher zone, being there mixed with other Schizophyceæ.

Microcoleus tenerrimus occurs in the tangled mats above mentioned, but is less abundant than the last species and has not been found in pure growths.

Oscillatoria limosa is frequently a sparse constituent of the matted coverings of the pebbles on the south shore of the Spit at 6 feet and upward (*e. g.,* at 500 east). Two other species also occur here, one of them distinguished from *O. limosa* by its constantly straight tips and the other by its smaller diameter, which is less than half of that of *O. limosa.*

It is probable that other species of *Oscillatoria* and of other Schizophyceæ which occur at higher levels will be found in the present belt, but the lack of time made it impossible to determine accurately the distribution of any but the more abundant species of these minute plants.

Rivularia atra forms shiny black pebbly patches, on otherwise bare, firm mud, between the 5 and 6 foot levels. It is most abundant on the vertical or overhanging bank formed by the caving off of the Marsh on the east side of the Creek at 100 to 200 south by 775 east. Here, in the shade of the overhanging grasses of the bank, many square decimeters of surface are covered more or less continuously by patches from half to several centimeters in diameter. These patches are distinguishable at once from those of the *Anabæna* mentioned above by their pebbly surface, greater thickness (1 to 2 mm.), and firmer texture.

Spirulina tenuissima is occasionally found rather sparsely mixed in the composite mats of green and blue-green algæ, seen in some parts of this belt, though both these and the *Spirulina* are more characteristic of higher levels.

BACILLARIALES.

Of the diatoms occurring on the beach and Marsh between 1.5 and 6.5 feet only two species have been noted as abundant. These are *Melosira* and *Pleurosigma.*

Melosira occurs usually sparingly in the mats and felts on pebbles or stalks of *Spartina* between the 4 and 6.5 foot levels. The filaments of *Melosira* found here are of many cells in length and are apparently in living condition. It is not certain whether this species propagates freely here or whether the filaments found arise from bits broken off from the epiphytic tufts on the *Zostera.*

Pleurosigma angulatum is found scattered over the felts of other algæ at and just above the 6-foot level.

CHLOROPHYCEÆ.

Of this group at least a dozen species have been found in the mid-littoral Marsh, some being quite abundant. (See plate VIII.)

Chætomorpha aerea forma *linum,* which we have mentioned as present on the bottom, is also found frequently mixed in the mats of *Rhizoclonium* about the *Spartina* stalks from 6 feet downward along the whole shore of the harbor.

Cladophora (*expansa?*) occurs abundantly about all four sides of the harbor from the 4-foot up to the 6.5 or even 7-foot level. In this habitat this species

is commonly sparsely branched, often simple for 15 or 20 cells. (The cells are 30 to 45μ wide by 200 to 600μ long. It is often found mixed with *Enteromorpha clathrata, Rhizoclonium, Vaucheria,* or various blue-green algæ, but it may also develop nearly pure growths, forming loose fluffy tufts on mud about the steps of *Spartina glabra* (*e. g.,* 2,000 north by 825 west). In the neighborhood of fresh-water rivulets this *Cladophora* keeps up 10 or 15 cm. above the level of the water during low tide. It evidently does not stand well a constant immersion in fresh water, though it must of course often be washed with rain-water during low tide. On April 8, 1911, no tufts of this alga were found along the shore. However, tangles of this same *Cladophora* were present in the Inlet on this date in great numbers. It seems certain that spores from these tufts must reach the shore, but find the conditions there less favorable than in the summer. This is probably because of the absence, in April, of the *Spartina* to give shade, to prevent desiccation, and also to hold the tangled threads of the alga.

Of the two species of *Enteromorpha* found in this zone *E. clathrata* is the most generally distributed. We have already noted that dense tangles, many yards in extent, may float up from among the *Zostera* and drift ashore to settle on the *Spartina,* crushing it down by their weight. Parts of the masses of *Enteromorpha* that sink in shaded places between the clumps of the *Spartina* may persist in a living condition for days or weeks. Far more important are the widespread smaller mats or tangles of *E. clathrata* covering the mud at the base of the *Spartina* stalks, either as pure growths or mixed with several other green or blue-green algæ. The *E. clathrata* of these mats adheres rather firmly to the mud, apparently by the silting in of its older parts. It has shorter branches and a smaller diameter than the tufted plants found on the *Zostera.* Streaming tufts, like those on the *Zostera,* are occasionally found in the present belt, in tide-pools (*e. g.,* at 0 south by 1,110 east at 3 feet and at 0 south by 1,165 east at the 4.5-foot level). In streams where the water is quite fresh for a considerable time at each low tide the *E. clathrata* is absent. It is found, however, at higher levels on the banks of such streams, out of reach of the fresh water (460 south by 680 east). In April 1911 this *Enteromorpha* was found on the stubble of the *Spartina,* but not nearly as abundant as it usually is in July and was in September 1911.

Enteromorpha crinita has been found between the 3 and 5 foot levels associated with *E. clathrata* and with *Rhizoclonium, e. g.,* on the eastern banks of the Creek at 200 south (see p. 59).

Enteromorpha intestinalis, the third species of this genus found in the harbor, is characteristic of just those habitats within this belt which are flooded with fresh water for from 5 to 10 hours at each low tide. In fact, this species is almost entirely confined to parts of the shore near fresh-water streams. Only a few smaller plants have been found elsewhere, as, for example, along the wharves, on stakes or buoys in the middle of the harbor, or in the channel to the Outer Harbor. The largest plants seen were those on pebbles in the tide-pools of the side-channel near 50 south by 590 east from 1.5-foot to the 2.5-foot levels. The water standing or running over these plants at low tide is but a decimeter or two in depth and is nearly or quite fresh. Under these conditions *E. intestinalis* reaches a diameter of 3 or 4 cm. and a length of 5 or 6 dm. In the Creek itself *E. intestinalis* is found scattered sparsely as far up as 450 south

at the 5-foot level, chiefly aside from the deepest parts of the channel. It is most abundant in rapids of this stream near 300 south at the 3-foot level, where it occurs along with *Monostroma* and living barnacles. These facts seem to indicate that the movement and aeration of the water are of advantage to the *Enteromorpha* or of disadvantage to its competitors, and that it can endure long immersion in fresh water. The densest stands of *E. intestinalis* found were those of the rapids of the Creek and those about the outlets of artesian wells on the east side (1,440 north and 1,535 north). We have already mentioned the *Enteromorpha* growing on the bottom near these well outlets. It is also found less abundantly on the wall of the wharf below these outlets, from the 1.5 to the 3-foot level. Here it is mixed with a *Monostroma* that crowds out the *Enteromorpha* from the part of the wall immediately below the outlets, which is actually flooded and not merely splashed with fresh water.

Another interesting type of habitat for *E. intestinalis* is found in the fresh-water rivulets that run down across the shore from the high-water mark (plate VIII). There are many of these on the west side of the harbor and several on the east side. The most interesting one on the latter side is the rivulet on top of the wharf at 1,000 north. The fresh water comes down through a ditch from a spring at some distance above the shore-line, and finally escapes between the big stones of the wall at the 5-foot level. In this stream *E. intestinalis* is found not merely among the *Spartina* on the bottom at 1.5 feet, but on the stones of the wall where washed by fresh water and also on the pebbles in the stream on top of the wharf, where at the 7-foot or 7.5-foot level, this alga is associated with *Scirpus americanus*, a characteristic plant of the upper littoral belt. This alga grows on pebbles and stones in the bottoms of streams on the west shore, where it is flooded with fresh water at low tide (1,050 north, 1,400 north, etc.). It often occurs here from the 7-foot level downward across the whole width of the mid-littoral belt.

On the banks of the little streams which are at all exposed to drying out at low tide, other algæ take the place of this *Enteromorpha*. In the pool below the flume of the mill at 500 north on the east side *E. intestinalis* grew at the 5-foot level where immersed in pure fresh water for 8 hours or more at each tide. Even at high tide the flow of fresh water was abundant enough probably to prevent the pool from ever becoming really salt. In this pool *Ascophyllum* was the only alga growing along with the *Enteromorpha*. In the fresh-water rivulets of the east and west sides of the harbor we find with *Enteromorpha* the red blotches of *Hildenbrandia* and several green algæ which form incrustations on the submerged pebbles. The association of *E. intestinalis* with fresh water is so characteristic about this harbor that one not only expects it wherever fresh water is found, but suspects the presence of fresh water wherever the alga occurs. Thus at 1,850 north, between the 2 and 5 foot levels, *E. intestinalis* occurs in a rivulet of water starting from about the 5.5-foot level. This water proved to be really fresh, and not merely salt water draining out of the marshy shore, as was at first supposed.

In all of those cases mentioned above where the *Enteromorpha* grows at or above the 7-foot level, it is evident that the alga must in the average tide be immersed in fresh water for 10 or 11 hours at each tide. Moreover, during each series of neap tides these plants may not be wet by salt water for several days. These facts, together with the fact that certain species of *Enteromorpha*

grow inland far from the sea, suggested the possibility that the present species might persist indefinitely in fresh water. Miss Stella G. Streeter, in the summer of 1910, attempted to determine this experimentally by moving pebbles bearing *E. intestinalis* to a point in the same stream above the reach of the tide. This resulted in the death of all plants thus subjected to a constant immersion in fresh water, in 16 or 18 days. Similar experiments with *Monostroma,* which is likewise associated with fresh water, showed that it is even less resistant to constant submergence in fresh water. The reason for the association of *Enteromorpha intestinalis* with fresh water has not been determined. It is conceivable that it may be because the *Enteromorpha* finds these habitats endurable for it and at the same time free from many competitors which it would encounter in really salt water. The fact that *E. intestinalis* grows in tide-streams, or on open shores, suggests also that the movement of the water in fresh-water streams may make these favorable habits.

Some observations were made on the rate of growth of sporelings of this species of *Enteromorpha* and *of E. clathrata.* Blocks of wood and stones placed beside *E. intestinalis* in its native habitat showed a crop of young plants from 1 to 2 mm. high in 3 weeks' time. Logs of a floating raft placed in the water on July 15 had many plants of *E. clathrata* on them by August 15, and they were 8 to 10 cm. long. The rate of growth in length of mature plants of *E. intestinalis* was also measured by Miss Streeter. In plants averaging 60 mm. in length at the start Miss Streeter found an average daily increase, during 20 days of observation, of 2.5 mm. The maximum daily increase observed was about 4 mm. Unfortunately these plants, even when left undisturbed in their native tide-pools, do not long withstand even the slight handling necessary for measuring them. In most of the plants the terminal portion began to die off in less than a week's time.

Ilea fulvescens is a second alga that is associated almost exclusively with fresh-water inlets of the Inner Harbor. This species forms smoky, olive green or brown flexuous threads, about 1 mm. in diameter and from 5 to 10 cm. long. It is found streaming from pebbles of the bottom, in the swiftest current, of these streams at levels between 1.5 and 7 feet above mean low water. It occurs most abundantly in the Creek, where in most years it covers many square meters of the bottom. In larger rivulets of the west shore *Ilea* has been found in one or two summers on constantly submerged pebbles between the 6 and 7-foot levels. It has also been found at one or two points on the south shore of the Spit. But here, instead of forming free streaming filaments, we find short threads of the *Ilea,* apparently in living condition, felted in with the other algæ that coat the pebbles of the beach between the 6 and 7 foot levels.

Why an alga so abundant each summer in the main stream should be relatively so scarce in the other streams about the harbor, it is difficult to understand. Apparently the conditions are closely similar in the two cases. On the other hand, it is not easy to see what common factors or conditions may determine the occurrence of this alga both in the fresh-water streams and on the beach of the Spit, since the latter is absolutely devoid of fresh water except such as falls in rain. *Ilea* is apparently an early summer form in this harbor; at least it was entirely wanting in the main stream, and absent from one or two of its other habitats on September 28, 1911.

Monostroma latissimum is a third green alga which is associated very constantly with fresh-water inlets about this harbor. This alga forms small sheets from a few millimeters to 5 or 6 cm. broad attached to pebbles of the bottom in most of the fresh-water streams about the shore, to rocks of the wharves below the fresh-water inlets, and more rarely to the stalks of *Spartina glabra* growing near fresh water. In the Creek the upper limit of *Monostroma* is found at 560 south by 820 east, at about the 6-foot level. It occurs here in the more quiet nooks along the banks, just out of the swiftest currents. The upper limit of its range is also at 6 feet in the small, very cold stream at 500 south by 860 east. A little farther north in the Creek it grows, across its whole width, on pebbles at the 4-foot level. From this point northward the *Monostroma* grows in midstream on shelly or pebbly bottom, down to the 1.5 or 1 foot level, at 140 south. In some of the small streams of the west shore, with colder water and more shade, this alga is found as high as the 7.5-foot level. The densest growth of *Monostroma* found is probably that near the overflow pipe of an artesian well, which penetrates the wall of the wharf at 1,440 north by 1,080 east, at the 5-foot level (plate VIII). This wall from 2 to 4.5 feet, where wet by the dripping or the splashing of the water, is covered by hundreds of the delicate sheets of this alga mixed with smaller numbers of *Enteromorpha intestinalis*. Similar though less dense growths of this alga are found at other points where fresh water flows over or through the wharf (1,025 north by 1,060 east and 2,075 north by 1,140 east).

A reference to the tide-chart (plate VI) will show that at the lowest limit mentioned above (1 to 1.5 feet), this alga will be submerged in salt water for 9 hours or less, according to the magnitude of the tide, and in fresh water for 3 hours or more. At the extreme upper limit (7.5 feet), on the contrary, it is evident that this alga is exposed to fresh water for several days continuously during each series of neap tides.

The chief competitors for standing room on substrata suitable for *Monostroma* are evidently *Enteromorpha intestinalis* and *Ilea fulvescens*. The former is abundant only near the lower limit of the *Monostroma* where the latter is sparse. The *Ilea*, on the contrary, is densest at just about the same levels in the stream, and under the same conditions of salinity as the *Monostroma*. In this region of approximation of these two species the rocks in the swiftest current are occupied by *Ilea*, for which habitat its filamentous form and lubricous surface especially fit it, while *Monostroma*, with its broad and relatively delicate sheets, lives in less turbulent water. The two species are actually found together in considerable numbers, chiefly in regions of moderately swift current. Shade, from plants along the banks of the stream, is apparently a factor less endurable by *Ilea* than by *Monostroma*.

The propagation of both species is evidently accomplished by zoospores, which must be capable of enduring immersion for some hours in salt water, while being transported about the harbor. This seems necessarily true, since *Monostroma* was practically wanting in April 1911, and yet had spread to most of the fresh-water rivulets in July. In September 1911 *Monostroma* was present in about the usual numbers in streams about the harbor and a few plants were found on the wharf of the Research Laboratory.

Rhizoclonium is a genus represented in the mid-littoral belt by two species, *R. riparium* and *R. tortuosum*, which occur, usually together, in somewhat

curly mats and tangles from the 2-foot level (*e. g.,* 35 south by 575 east) upward, to and beyond the upper limit of this zone, as, *e. g.,* along the west shore, where it reaches to 5, 6, or even 7 feet. These tangles include, beside the *Rhizoclonium,* smaller amounts of each of a few species of green algæ and of many species of blue-green algæ, all of which we have referred to above. The tangles are sometimes twisted more or less tightly about the stalks of *Spartina glabra* and sometimes form rather closer mats on the mud, at the base of the *Spartina* stalks, or in tide-pools from which *Spartina* is absent. In still other places, *e. g.,* along the steep eastern bank of the Creek at 200 south, between the 3 and 5 foot levels, these algæ occur either in an almost pure growth, or mingled with *Enteromorpha crinita,* and are woven into almost continuous sheets, sometimes 2 or 3 dm. wide, a millimeter or two in thickness, and often a meter or two in length. These algal curtains probably start as a coating over the surface of the vertical or overhanging bank, which is formed by the caving off of the peaty mud of the high Marsh east of the stream. The filmy covering formed at first in contact with the mud apparently peels off below and hangs vertically, supported by the adherent upper edge. Growth may still continue in these pendant sheets, which are immersed from 4.33 to 6.5 hours each tide, and are kept moist during low tide by the water dripping from the bank above.

A very marked peculiarity of this alga is its evident inability to endure long immersion in fresh water, although it exists in brackish water. Along each fresh-water rivulet the lower edge of the mat of *Rhizoclonium* remains a few centimeters above the level of the fresh water at low tide. The same thing is shown by its absence from those areas of the main stream which are covered by fresh water at low tide, though it does occur on the edges of the tide-pool at 35 south by 575 east at 2 feet. This pool has 6 inches of brackish water in it at low tide.

In April 1911, *Rhizoclonium* seemed to be about as abundant and in the same places as in July and September 1911. This seems to show clearly that *Rhizoclonium* is a perennial alga. It is the only monosiphonous cellular form on shore and wharf in the summer, but in April another somewhat similar alga *(Ulothrix flacca)* was abundant on wharves and on branches of the *Ascophyllum, Fucus,* and *Pylaiella* that are attached to the wharves.

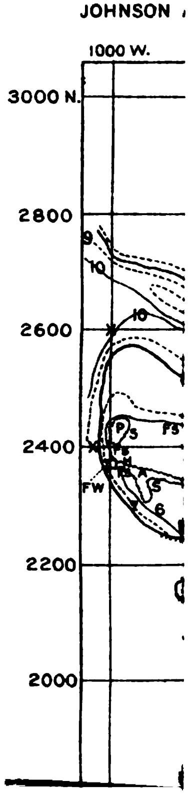
Ulva lactuca latissima, as we have seen, is most characteristic of areas below 1.5 feet, that is, of the harbor bottom. It occurs, though much less abundantly, in the present belt also. A few plants grow on wharves or stakes, but it is found chiefly along streams or in tide-pools, where it is not dried out at low tide. Up to the 3 or 4 foot level, considerable numbers of detached plants are found in tide-pools. In the pool at 35 south by 575 east it occurs at the 2-foot level, in water that is brackish at low tide. At 2,800 north by 650 east, at the 4-foot level, is a tide-pool with hundreds of detached plants of *Ulva,* which are but a few decimeters broad, very much curled and perforated by numerous roundish holes a centimeter or more across. This type, which somewhat resembles var. *mesenteriformia* of Collins, occurs in a few other places where the water becomes much heated by the sun during low tide. It is found, *e. g.,* in small pools along the tide-stream through the *Spartina* at the east end of the Spit near 800 east, and less-developed examples of this variety occur along the northern border of the *Spartina* zone near 0 to 150 north by 400 to 500 east. The

one other habitat in which *Ulva* occurs in this mid-littoral belt is along the edges of fresh-water streams and rivulets. Here the plants are attached to pebbles, shells, or stems of *Spartina*. For example, in the Creek the southern limit of *Ulva* is between 100 and 200 south. Here it occurs along the stream-edges at the 1-foot level, just above the surface at low tide, where the water is quite fresh. Northward from this point the alga becomes more and more abundant up to 200 north, where there is a dense growth of *Ulva*, especially on the east side of the channel. Only a few plants occur here, even in the channel where constantly submerged. In the small rivulets on the east and west sides of the harbor *Ulva* is found up to the 3.5 or 4 foot level, on immersed pebbles or on stalks of the neighboring *Spartina* where shaded by this grass. The *Ulva* is confined to those parts of the mid-littoral belt where the substratum, or perhaps the surrounding air, is unusually moist, and thus prevents the drying out of the plant at low tide. This view seems confirmed by the fact that in April 1911 numerous small plants of *Ulva* were found attached to the dead stubble of the *Spartina* all along the west shore, where, except near the rivulets, *Ulva* was wanting entirely in July, August, and September 1911.

Vaucheria (thuretii?) is the last species of green alga to be mentioned as occurring on the shores of the mid-littoral belt. It is found either in nearly pure tufts or as a constituent of the compound felts referred to above, which are made up primarily of *Rhizoclonium, Enteromorpha clathrata, Cladophora,* and *Lyngbya æstuarii*. These composite felts including *Vaucheria* are found quite generally on all four sides of the harbor between the 5 and 7.5 foot levels. The *Vaucheria* is usually found in felts that are more or less protected from desiccation by shade or by unusual wetness of the soil. The pure tufts are most abundant on the south and west sides and have not been seen at all on the Spit. The only considerable patches seen are near fresh-water inlets, though never so near as to be submerged in fresh water for more than an hour or so at each tide. Good examples of these turfs are the dark-green ones, a meter or more square, found on the banks of the Creek, at 300 south by 790 east at the 4-foot level; at 400 south by 800 east at 5 to 6 feet, and that near 500 south by 750 east at 6 feet. A seeming exception to this constant association of the *Vaucheria* turfs with fresh water is found at 1,714 north on the west shore at 6 to 6.5 feet. But though no fresh water is running over the surface at this point, it *is* seeping through the soil in quantity sufficient to make the soil-water here at low tide decidedly less saline than the water of the Spit beach or the water of the harbor. In speaking of the occurrence of *Lilæopsis* at this point, we have already mentioned the fact that small trickles of fresh water come out of the beach between the 4 and 5 foot levels.

The turfs of *Vaucheria* are also found in wet places in the upper littoral levels of the Marsh south of the harbor, in wet areas near tide-pools, or where the water is apparently coming up from below.

From the observations above given it seems evident that the presence of an unusual amount of water in the soil, even though it be fresh water, serves to protect the overlying *Vaucheria* from drying out. In the composite felt on the drier beaches, the other more resistant algæ probably serve to protect the more delicate *Vaucheria*, and thus enable it to live higher up the beach than it could otherwise do. This same sort of protection is sometimes given to the *Vaucheria* at higher levels by the *Spartina patens*, as from 150 to 250 south and between


JOHNSON
1000 W.
3000 N.
2800
2600
2400
2200
2000
10
FW

400 and 600 east at the 6.5 to the 7.5-foot levels. There is possibly also some subterranean fresh water in the soil of this area, for it comes out in rivulets just south of this.

PHÆOPHYCEÆ.

The most prominent brown algæ of the mid-littoral marsh are *Ascophyllum* and *Fucus*. These are the same species that dominate the same levels (1.5 to 6.5 feet) on the walls of the wharves. On this marshy belt, however, these algæ nowhere form a pure stand over any considerable area, since there are no extensive stony beaches to give them a satisfactory footing. Only on the east side of the Inlet and on an occasional log, stone, or shell about the other shores of the harbor do these algæ find, between these levels, a satisfactory substratum for attachment. (For distribution see plate IX.)

Ascophyllum nodosum is scattered about the whole circumference of the harbor, and throughout the entire width of the present belt. At the lower levels it has much the same size and coarseness as on the wharves. At the upper levels, especially in places exposed to high temperatures, this alga remains smaller and the branches are much more slender than those of the plants growing on the wharves. On the shore, as on the wharves, ripe receptacles are rare during the summer, though abundant during the spring. The distribution of *Ascophyllum* in relation to fresh water is seen best along the natural shore. By the main stream, from 10 north to 600 east, etc., *Ascophyllum* grows 2 feet long and is fertile, but it keeps just above the level of the fresh-water stream at low water. Again, at 1,000 north on the east shore, there is a vertical strip of stone wall 3 feet wide, horizontally, that is bare of *Ascophyllum,* where a fresh-water stream runs through the wall. In the pool of fresh water just south of the mill, *Ascophyllum* is found on logs and stones about the border, but always just above the level of the surface of the pool at low water, which is at 5 feet. Only at two spots along the eastern side of the harbor (1,435 north and 2,050 north), where the water from artesian wells flows over or between the pebbles of the bottom, does *Ascophyllum* seem to grow where it is wetted with running or splashing fresh water at low tide. Closer examination of the plants near the outflow from these wells shows that only part of the thallus is actually submerged in the fresh water during any one low tide. The other branches are held above the water by the submerged ones and by those stones and pebbles between which the water is flowing, as they would not be in the more definite channels of the streams along the natural shore of the harbor. In the spray-zone also not all parts of the surface of a plant are completely flooded all the time. On the whole, it seems evident that these plants of *Ascophyllum,* in common with those of the wharves and shore, are really enabled to carry on some gaseous exchange with the air during low tide. It must, of course, be remembered also that in the turbid water of the Inner Harbor the light supply of even slightly submerged plants would be greatly diminished. The exclusion of light would probably be just as efficient a cause in keeping *Ascophyllum* above low-water level as would be the cutting off of the more ready access to CO_2. We may note also that while the lower limit, in the Inner Harbor, of *Ascophyllum* and its associate *Fucus* is about 1 to 1.5 feet above mean low water, they occur at 1 or 1.5 feet below mean low water on the rocky beaches of Long Island Sound. In this latter habitat the water is much clearer and so would allow more light to reach plants that are continuously submerged, as some of these plants of *Ascophyllum* and *Fucus* must be for

several tides in succession, during each series of neap tides. But the water of these open shores is also much better aerated by the constant movement, and thus may furnish a much better supply of the necessary oxygen and CO_2 to a submerged plant than it could obtain from the water of the Inner Harbor. It is also true that the paraphyses of *Fucus,* for example, are much better developed on plants in the Sound, which may perhaps aid in the absorption of CO_2 from the water. Nowhere in the neighboring parts of the Sound have *Ascophyllum* or *Fucus* been found at more than 2 or 3 feet below mean low water. The same inability of these plants to withstand constant submergence is indicated by their absence from tide-pools. This has been noted in the cold water of Casco Bay, Maine, as well as at Cold Spring Harbor.

It seems clear that the absence of *Ascophyllum* or *Fucus* below the 1-foot level in the Inner Harbor may be due either to the insufficient light or the insufficient opportunity of gaseous interchange. Only a carefully planned study of the problem can show definitely just how far each of these factors is concerned in determining this lower limit.

Two species of *Fucus (F. evanescens* and *F. vesiculosus)* are distributed about the harbor in this mid-littoral belt. These are found along with the *Ascophyllum* wherever a stone, a sunken log, or a shell, including the shells of living mussels, gives them a footing. *F. evanescens* occurs rather rarely on large stones in open places.

Fucus vesiculosus is far more abundant and widely distributed, and is represented by at least three distinct varieties. The typical form of the species, the robust one characteristic of the vertical walls of the wharves, occurs also on stones of the bottom. These latter are chiefly stones that have fallen from the wharves, and are especially abundant along the east side of the harbor. But this robust *Fucus* is also found on larger pebbles and stones in the lower parts of this belt far from the wharves, for example, in the Inlet or less frequently along the west shore from 600 to 2,200 north. The distribution of *F. evanescens* and of the typical *F. vesiculosus* is in general similar to that of *Ascophyllum,* except that they may grow at somewhat higher levels. Their distribution is apparently determined by the same factors that affect *Ascophyllum.*

The variety of *F. vesiculosus* which is most widely distributed on the marshy shore is a more slender form (probably *F. vesiculosus laterifructus* Grev.). This variety grows in habitats between the 1.5 and 6 foot levels that are more or less shaded by *Spartina glabra.* The fronds of this *Fucus* are attached either to pebbles or shells, and never, so far as seen, to the stalks of the *Spartina.* Nowhere does this variety become as dwarfed and attenuated as it does on the muddy shores of certain more protected near-by harbors, such as Lloyd's Harbor. In this variety of *Fucus* we have another excellent opportunity for an experimental study of the factors determining a particular type of plant structure. (Plate XVI B.)

Perhaps the most interesting variety of *Fucus* found about the harbor is *F. vesiculosus* var. *spiralis* (L.) Ag. (plate XVI A). This form occurs between the 1.5 and 6 foot levels, chiefly along the west and north shores of the harbor. It is sparse in the fringing Marsh at 50 to 150 north by 700 to 1,000 east and is most abundant in the large *Spartina* area south of the east end of the Sandspit, where scores of plants occur tangled together in a single square meter. This variety differs from all the other forms of *Fucus* mentioned in habit, since it is

not attached by holdfasts, but simply lies in curly, twisted tangles among the stems of the *Spartina*. It also differs from these markedly in structure. The individual plants vary in length from 1 to 3 dm., and have a nearly constant width from end to end of about 8 mm. The midrib is not at all prominent, cryptostomata and vesicles are rare, and fruiting branches have never been seen on this variety here during the summer season, nor on the April and October visits. From the absence of any receptacles on the older plants and also of any sporelings or very young plants, it seems evident that this variety does not frequently propagate itself sexually. From the mode of growth of this alga, in tangles not attached by holdfasts, and from the occurrence of small broken-off bits floating about in the water, it is highly probable that the chief mode of propagation is this purely vegetative one, resembling that of the well-known *Sargassum bacciferum*.

The question now arises concerning the relation of this form to the typical *F. vesiculosus*. In view of the absence of receptacles on *F. spiralis*, the suggestion occurs that the plants of this variety may ultimately arise only from oöspores or fragments of typical plants of *F. vesiculosus*. Portions of the thallus of this species of the variety growing on the wharves were tangled in wire netting and left for four weeks among the *Spartina* on the Spit. At the end of this time the tips of most of the plants had begun to assume the characteristic spiral twist of the variety *spiralis*. In the following spring some of the spiral plants developed from the fragments showed 4 inches of spirally twisted thallus. It may be noted also that plants having essentially the vegetative character of *F. vesiculosus spiralis* were found by the senior writer at Quahog Bay, Sebascodegan Island, Maine, in August 1911. These plants were attached and bore well-developed receptacles. The occurrence of fertile plants in these colder waters in summer suggests that the plants at Cold Spring Harbor may be fertile during the winter. But it seems hard to believe that no trace of the fertile branches should remain on July 1 or be initiated by late September. Unfortunately, no thorough search was made for them in April 1911.

Ectocarpus is the only other brown alga recorded in this belt between 1.5 and 6.5 feet on the natural shores of the harbor. It occurs sparsely and locally at 0 south by 670 east between the 5 and 6 foot levels. It is matted with *Rhizoclonium* at 35 south by 575 east. This is apparently identical with the *Ectocarpus* occurring in the deep part of the channel of the Creek about 150 feet south of the last-mentioned locality. It is possible that the plants were simply broken-off portions floated by the water to the spots where they were found. But the filaments recorded seemed to be living and growing.

RHODOPHYCEÆ.

The only red algæ that have been found growing above the 1.5-foot level are *Bostrychia rivularis, Delesseria leprieurii, Hildenbrandia prototypus, Petrocelis (cruenta?)*, and *Porphyra laciniata*. All of these except *Porphyra* have been recorded from among the *Spartina* of the Mid-littoral Marsh, but only *Hildenbrandia* is at all frequent in summer.

Bostrychia rivularis, although abundant on the rocks and piles of the wharves at all seasons, has been found in the *Spartina* marsh but once. This was in September 1911, when a patch of several square decimeters was found growing on a sunken log among the *Spartina* just north of the wharf of the Research

Laboratory. Other tufts of it were found at the same point growing as epiphytes on *Fucus* and *Ascophyllum* attached to the same log. *Bostrychia* rarely assumes this epiphytic habit in summer, but in fall, winter, and spring it is common on the rockweeds, as we shall see when discussing in detail the algæ of the wharves.

Delesseria leprieurii is a small, smoky green alga 2 or 3 cm. high, which has been found only occasionally. It was first recorded in 1908 as growing on a sunken log at the 4-foot level near 250 north by 1,000 east. It was recorded but once again (1,750 north by 1,080 east at 1-foot) until September 1911, when it was found abundantly on a number of logs along the west shore between 1,200 and 1,500 north near the 3 or 4 foot levels. This alga, like *Bostrychia,* has not been found among the *Spartina* stalks, as it apparently was by Holden (see Collins, 1905). It is barely posisible that one or both of them may occur in this habitat during the fall or spring, but the rather hurried searches made for them at these seasons have failed to reveal them. *Delesseria* is perhaps the best example that we have found at Cold Spring Harbor of an alga that is transient in character. It occurs in considerable abundance in one or more places in any given season and may be wanting in any one of these places or even in the whole harbor in other seasons.

B. THE MID-LITTORAL ROCKWEED ASSOCIATION, ON WHARVES BETWEEN 1.5 AND 6.5 FEET.

The part of the mid-littoral belt that we are now to discuss is one showing quite definite vertical limits and characterized by a considerable number of algæ, which are largely restricted to the wharves. There are also certain others which, though they may occur sparingly below this belt, or elsewhere within it, never reach their fullest vigor or luxuriance except on the walls of the wharves. It might be expected that the more natural portions of the harbor boundary would offer the best opportunity for studying the distribution of algæ in the harbor. As a matter of fact, the walls of the wharves form the only considerable area of proper substratum for many of the algæ characteristic of this belt. These areas are therefore the only ones offering adequate opportunity for the study of the vertical distribution of some of the most important species in this belt, and of the factors determining this distribution.

About 20 species of algæ have been recorded as occurring on the stones, piles, and logs of the docks and wharves, and on parts of wrecks. A few species of *Calothrix* and *Lyngbya* here mentioned are more abundant just above the upper limit of our belt, but are mentioned here only for the sake of brevity. These species, arranged in systematic order, are the following:

Schizophyceæ: *Calothrix* (2 species), *Lyngbya* (2 species), *Oscillatoria* (sp. 1), and *Rivularia.*

Chlorophycææ: *Bryopsis plumosa, Monostroma* (sp.?), *Rhizoclonium* (2 species), *Ulothrix flacca, Ulva lactuca.*

Phæophyceæ: *Ascophyllum nodosum, Fucus platycarpus, F. vesiculosus, Pylaiella littoralis robustus,* and *Ralfsia clavata.*

Rhodophyceæ: *Bostrychia rivularis, Delesseria leprieurii, Hildenbrandia prototypus,* and *Porphyra laciniata.*

By far the most prominent algæ on these wharves are *Ascophyllum* and the two species of *Fucus,* while *Rhizoclonium* and *Bostrychia* come next in abun-

dance and in widespread distribution, though less noticeable because of their size.

The two rockweeds together cover from two-thirds to nine-tenths of the surface of the walls of these wharves, from 8 to 12 inches above the bottom up to 6.5 feet. The bottom of the harbor, near all of these wharves, except those by the Inlet and that of the Research Laboratory, is about 1.5 to 2 feet above mean low water. The lowest rockweeds are attached at about the 2.5 or 3 foot level, and thus hang down at low tide until their tips lie on the mud, and so they actually cover the walls all the way down to the bottom. Hence, as one looks at the walls at low tide, he sees a brown band of rockweeds starting at the bottom and ending above with the thinned-out *Fucus,* quite constantly between 6.5 and 7 feet above mean low water (plate XVII).

While *Fucus* may occur throughout the whole width of this belt, *Ascophyllum* is usually confined to levels below the 5.5 or 6 foot levels. That is, the upper 12 or 15 inches of the rockweed belt consists of *Fucus* alone, or of *Fucus* interspersed with a few plants of *Ascophyllum,* and with the relatively inconspicuous *Rhizoclonium* and *Bostrychia.* In the lower 3 or 4 feet of the zone *Ascophyllum* makes up from 50 to 90 per cent of the conspicuous brown covering of the walls. Thus at 1,550 north on the east side, a vertical strip of the bottom and wall a foot in width showed the neighboring bottom to be well covered with *Ulva.* The portion of the wall between 1.5 and 5 feet bore 150 plants of *Ascophyllum,* and above the 5-foot level there were 120 plants or plantlets of *Fucus* besides *Rhizoclonium* and a few tufts of *Bostrychia.*

On some wharves a band of *Rhizoclonium* 0.5 to 0.7 foot high is found above the rockweeds. This band, which often includes some matted *Lyngbyas* and *Calothrix,* is frequently interrupted and not prominent when viewed from any great distance.

In general then, the rockweed band is nearly continuous on the east side of the harbor from 500 to 2,800 north. (See plate XVIII A.) On the south it extends from 0 to 370 east and on the west side it is found from 0 to 550 north, from 1,060 to 1,220 north, and from 2,090 to 2,240 north. This rockweed band differs little in general character on different wharves except that its lower boundary is higher on wharves where the neighboring bottom is high (as between 200 and 300 east, at the south end of the harbor). The upper border may be unusually high on well-shaded walls. For example, in the southwest corner of the harbor from 0 to 20 south by 0 to 200 east the uppermost *Fucus* occasionally grows as high as 7 feet, or even slightly above this where attached to the undersides of the stones and logs of the wharves or in the cracks between them. The density of the stand of these rockweeds on the wharves near the Biological Laboratory has been somewhat lessened by the removal of several boatloads each year to be used for the annual clambake at the Laboratory. The *Fucus* and *Ascophyllum* are pulled off, leaving only the holdfast and more or less of the basal part of the plant adhering to the wall. The renewal of the covering on the wall is due in large part to the development of new fronds from these stumps of the old plants. Such an annual cleaning off also, of course, gives sporelings a better chance to get started without being shaded out.

Miss Streeter has discovered that a regeneration, similar to that mentioned above, occurs when the growing tips of either *Ascophyllum* or *Fucus* are eaten off by snails *(Paludina),* as they frequently are.

It is evident that the rockweed covering of the wall may be pretty completely renewed by this sort of regeneration each year, if we assume that the rate of growth found by Miss Streeter for July is continued for most of the year. In careful measurements of the elongations of plants of *Fucus* varying from 1 to 20 cm. in length, made daily for a month or more, Miss Streeter found an average daily growth varying from 0.5 to 1 mm. in different plants. Observations on the rate of growth of sporelings, however, as determined by the measurement of the same young individuals at periods 3 months apart, and by the time taken to cover a piece of new wall, indicates that the covering of the wharf near the Laboratory could not be renewed in a year's time.

With the above-noted general characters of the rockweed association in mind, we will now discuss the individual species of which it is composed, in the systematic order indicated on page 64.

SCHIZOPHYCEÆ.

Most of the members of this group found in the rockweed association occur in small blackish felts or gelatinous patches, occasionally on stones, but chiefly on piles or dock logs. The peculiarities of each species of this class are indicated below.

Calothrix fusco violacea occurs in blackish felts 1 or 2 cm. wide, several centimeters long and 1 to 2 mm. thick. This has been found rather generally about the harbor between the 6 and 8 foot levels, on stone (as at 1,050 north by 450 west at 6.5-foot) or on wood (as at 2,200 north by 1,230 east near the 7.5-foot level). At these levels it is evident that the plants must withstand long exposure to desiccation and to rain, the last habitat mentioned above being the high-water line of neap tides. It is noteworthy also that this species seems to grow higher on wood, which has the capacity for absorbing and conducting water more readily, and therefore probably keeps the algæ more moist when above the water-level than they would be on stone. Another *Calothrix,* which resembles *C. scopulorum* in the size of its cells, was found under the mill at 500 north by 1,000 east at the 6 to 7 foot levels, on a wooden post, wet by a spray of fresh water at low tide and by salt water at high tide. *Calothrix crustacea prolifera* occurs between 7 and 8 feet on logs of the Research Laboratory Wharf.

Lyngbya sp. was found on the post just referred to above.

Lyngbya (sp. 2 to 4.5μ in diameter, with tortuous tips) formed felts 1 mm. or more thick on the same post and on piles and pieces of wreck between 1,100 and 1,230 north on the west shore at the 6.5 to the 7 foot level.

Oscillatoria (at least two species) was found at the 7-foot level on the wharf of the Research Laboratory, on the wreck just south of it, and also on the bell of an hydraulic ram operated by fresh water near 2,830 north on the west shore.

Rivularia (sp.?) formed dozens of blackish gelatinous disks 0.5 cm. in diameter on logs of a wreck at 1,240 north by 575 west, between the 6 and 7 foot levels.

These few blue-green algæ were not especially sought for on all the wharves about the harbor, and hence might possibly have been found elsewhere in some seasons. Perhaps each of them may be found to be generally, though sparsely, distributed on similar substrata at similar levels. Several of them, in fact, were found on the beaches between the same levels. We are clearly safe in concluding that the species of these simple algæ are confined, like most other

plants of the harbor, within definite and quite restricted tide-levels, though here, as with other forms, it will take further study to distinguish the exact factors determining distribution.

CHLOROPHYCEÆ.

The only species of this group which are at all prominent on the wharves are *Rhizoclonium tortuosum* and *R. riparium*, except for *Ulothrix flacca*, which is abundant in winter. The first two algæ are more abundant and widely distributed on the wharves than any other algæ save *Ascophyllum* and *Fucus* (see plate VIII).

Rhizoclonium: The two species of this genus form a distinct green band above the upper margin of the rockweed zone, including some of the wall surface within the mid-littoral belt, and often extending some inches above this. The upper limit of *Rhizoclonium* in more exposed places may be at 6.75 or 7 feet, while in more protected places between stones of docks, on the north side of a wharf, or on projecting stones or piles, it may get up to 7.5 feet. In rare instances, when the places are very well protected, it may go even to 8 feet. The lower limit of this alga, where there are otherwise unoccupied spots on stones or piles, is at 3 or 3.5 feet. In those rare and small areas about the wharves where *Fucus* or *Ascophyllum* are nearly or entirely wanting over the whole vertical height of the wharf, the *Rhizoclonium* may form a distinct though thin green band on the wall 3 or 4 feet in vertical width.

Any of the various kinds of rock in the walls seem to furnish a suitable substratum for the *Rhizocloniums*. The upper limit of distribution of *Rhizoclonium* is apparently determined chiefly by the amount of desiccation which it can endure. This is evidently dependent not only upon the level at which the plant grows, but also on the direction in which the wall faces and the presence of damp and shaded crevices between the stones of the wharf. The usual absence of *Rhizoclonium* below 6.5 or 6 feet is due to the presence there of its more vigorous competitors, *Fucus* and *Ascophyllum*. In those places where *Fucus* and *Ascophyllum* are absent and *Rhizoclonium* present, the lower limit of the green alga is perhaps determined by the long submergence of habitats below the 3-foot level. This may well be of considerable importance in a harbor where the water is usually decidedly turbid near the wharf. This water is relatively opaque to light, and thus would prevent, or diminish, photosynthetic activity in the *Rhizoclonium* during some 6 or 7 hours each tide. We shall note facts later which indicate that these same factors are concerned in determining the limits of this alga on the beach and Marsh. In April 1911, *Rhizoclonium* seemed just about as abundant as in July, and with the same distribution.

The other species of green algæ found on the wharves, save the epiphytic *Ulothrix flacca*, occur either singly and widely scattered or in strictly local and usually small groups. We will take these up for brief discussion, in alphabetical sequence.

Bryopsis plumosa: This alga has been seen but three times, and then it was on the east side of the Inlet at the 3-foot level. Only two or three tufts of it were found here, though it is scattered generally in the Outer Harbor, and scores of dense clumps of it are found each summer in a tide-stream entering the Outer Harbor 3 miles north of the Inlet.

Monostroma latissimum: This species is found on the wharves only at the relatively few points where small streams of fresh water trickle over or through the wall of the wharf. Just below the artesian-well outlet at 1,435 north on the east shore, the wall is covered pretty thickly for a width of 0.5 meter or more between the 5-foot and 2-foot tide-levels, with plants of *Monostroma* which are 4 or 5 cm. long. These plants are submerged in salt water from 5 to 8 hours each tide, and exposed to the dripping fresh water or its spray for the rest of each tide, about 8 to 5 hours. Another fresh-water outlet at 1,010 north on the east side has, in most summers, a colony of *Monostroma,* both on the rocks of the wall and on the pebbles of the stream-bed at the 7 or 7.5 foot levels. Finally, *Monostroma* occurs on the brick-work about the fresh-water ram at 2,380 north by 990 west, from the 7-foot down to the 4-foot level. The factors influencing the distribution of *Monostroma* have been discussed in speaking of the mid-littoral beach or shore.

Ulothrix: Of this genus *U.* (*implexa* Kutz?) has been found two or three times each summer in the neighborhood of fresh water, *e. g.,* between the 6 and 7 foot levels on piles under the mill at 500 north by 1,000 east, which are wet by spray from the mill-wheel. It is also found at the 7-foot level on pebbles in the fresh-water stream at 1,010 north on the east side.

Ulothrix flacca is a form which has not been found in the summer, but which was very abundant as an epiphyte and less frequent on logs and piles in April 1911. The short, simple filaments of this alga at that time formed thin, grayish-green turfs over the woodwork of the wharves about the harbor. It has never been seen in these locations, or elsewhere in the harbor, in July or August. As an epiphyte on *Ascophyllum* or *Fucus* it forms a greenish coating of short filaments over that surface of the flat frond which is usually exposed to the light as the rockweed hangs down beside the wall at low tide. What is apparenly the same alga also forms long, lubricous tufts on the fertile clubs of both rockweeds in April. It was also frequent at this season as an epiphyte on *Pylaiella,* which flourished in great numbers along the Inlet. The absence of this epiphytic *Ulothrix* from the rockweeds in summer seems probably due to its inability to withstand the more severe desiccation during low tide at this season, though this has not been proven experimentally.

Ulva lactuca: This is the only green alga of the wharves remaining for us to discuss. This species we have found to be abundant on the harbor bottom, and frequent also on the mid-littoral marsh, up to the 4-foot level, but it occurs only infrequently on the wharves. A few small plants have been found scattered about the wharf of the Research Laboratory, and still fewer on other wharves. Even in April 1911, when young plants of *Ulva* were very numerous in the Inlet, they seemed to be no more frequent on the wharves. From observations thus far made it is impossible to decide whether the scarcity of *Ulva* on the wharves is due chiefly to the competition of the rockweeds or is directly due to the exposure to desiccation at these levels. In view of the slow growth of the rockweeds and rapid growth of the *Ulva,* it seems probable that the latter might, at least temporarily, occupy the spots bared of rockweed by the ice, were it not for the long exposure to desiccation it would experience on most of these walls.

A. South Shore of Spit (300 to 600 East), showing Path worn by Pedestrians, near 7-foot level, through a Vegetation of *Limonium*, *Sueda*, *Salicornia*, etc. *Spartina glabra* at right. *Œnothera*, *Solidago*, and *Rhus glabra* at extreme left.

B. *Salicornia ambigua* and *Limonium* (in bloom) on South Shore of Spit. Among and over the Pebbles Algal Felts are Present.

PHÆOPHYCEÆ.

We have already seen that two brown algæ, the rockweeds *Ascophyllum* and *Fucus,* give character to the mid-littoral belt on the wharves. We will now, in somewhat more detail, take up the distribution of these and the other Phæophyceæ occurring on the wharves. (See also plate IX.)

Ascophyllum: Plants of this alga of all lengths from 1 or 2 cm. up to 0.5 meter or more are found in the harbor at all seasons. In July or August fertile branches or receptacles are infrequent on plants of the Inner Harbor, and mature ones have not been seen. In April 1911, plants with fertile clubs were numerous and these receptacles bore an abundance of ripe antheridia and oögonia. At this early spring season the receptacles were often covered by a turf of *Ulothrix flacca.* In some places *Ascophyllum* may form nearly pure patches between 3 and 5.5 or 6 feet, with 20 or more plants per square foot (plate XVII). In other areas it may be mingled more or less equally with *Fucus,* the two together covering the wall of the wharf. In still other places there may be considerable gaps in the rockweed belt oftenest filled with *Bostrychia* or *Rhizoclonium.* The rockweeds are probably ground off from these spots by boats and ice, and the clean surface so formed is then occupied at once by those algæ whose spores happen to be ready for attachment and germination at just that time. There seems to be no difference in the capacity of *Fucus* and *Ascophyllum* to grow upon a given substratum within the range of the *Ascophyllum.* There seems also to be some competition between the two, arising from the shading out of young plants of the one by older ones of the other. Then too the plants of *Ascophyllum,* being larger, may finally overgrow and shade out even older plants of *Fucus.* It is pretty certain also that the heavier *Ascophyllum* often tangles with the *Fucus* and finally tears it loose.

The substrata upon which *Ascophyllum* occurs include wood, shells, sandstone, some kinds of granite, and gneiss. On the wharves of the east side, however, it was noted that certain large yellow granite stones, between 1,000 and 1,600 north, contrasted strongly with the dark sandstone, gneiss, and schist of the rest of the wall, in being entirely bare of *Ascophyllum* and *Fucus,* even where the immediately adjoining stones of the wall above, at the sides, and below, were densely covered with these rockweeds (plate III B). The general chemical character of the barren blocks of granite, we are told by a competent petrographer, is essentially like that of the well-covered blocks of gneiss and darker granite. Moreover, the physical character of the barren stones does not seem sufficiently unlike that of the covered ones to explain the barrenness of the former.

Ascophyllum grows only in salt or brackish water, but it is capable also of enduring wetting by splashing fresh water or even by submergence of parts of the plant in fresh water for 2 or 3 hours of each tide. We have mentioned above (p. 61) its occurrence near the outlet of the artesian wells at 1,435 north on the east side. Perhaps different branches of each plant may be immersed in successive low tides. In another habitat on the east side, namely, the fresh-water pool just south of the mill, *Ascophyllum* does not grow below 5 feet, the level of the fresh water at low tide, but it does grow just above this where exposed to the air or even to a spray of fresh water for 7 or 8 hours each tide. At 1,010 north on the east shore the rocks of the wharf washed by fresh water from the entering stream are bare of *Ascophyllum.* As a last example, plants of this alga

0.5 meter long were found just at the edge of the main stream at 10 north by 600 east where it is washed by fresh water for 2 or 3 hours each tide.

From these examples it is evident that while *Ascophyllum* will not withstand constant submergence in fresh water, it can endure submergence in it for 2 or 3 hours each tide, provided that it is immersed in salt water for the rest of the tide. On parts of the wharf walls not exposed to fresh water the denser growth of *Ascophyllum* usually ceases at about 5.5 feet, but oöspores germinate at considerably higher levels in protected places between rocks or under the shade of the more hardy *Fucus*. As these young *Ascophyllum* plants grow, however, and push out from under these protecting objects, they are subjected to severe desiccation during the long exposure to the air. Most of the plants that have started at these higher levels are killed off, and those that persist are few and dwarfed. The highest plants of *Ascophyllum* found were always in places protected from extreme desiccation by northern exposure or overshadowing rocks, piles, or *Fucus*. It seems clear that the upper limit of distribution of *Ascophyllum* is determined by the time of exposure to the air, though it is true that *Ascophyllum*, like *Fucus*, may endure drying out until it becomes brittle enough to crush, almost to powder, in the hand.

The lower limit of *Ascophyllum* on the wharves, which is usually at 1 foot or more above the bottom of the wall, is probably determined by the injury, by burial in the soft mud, to those plants that grow nearer the bottom than this. Where the bottom is stony, as at 2,000 to 2,600 north, on the east side, we have already noted that the *Ascophyllum* goes to the extreme lower edge of the wall and then continues on over the stones of the bottom down to mean low water, below which it is very rarely found. (See plate XVIII A.)

Fucus: The two species found are not distinguishable by grosser characters that can be seen as the plants hang on the wharves. We shall therefore simply record the distribution of the genus without attempting to distinguish the species. The plants of *Fucus* found vary in size from young sporelings to plants 2 or 3 dm. long, and with main branches 15 or 20 mm. broad (plate XVIII B). They occur on all the substrata bearing *Ascophyllum*, that is, on stones, shells, and piles. *Fucus*, like *Ascophyllum*, is distributed almost continuously along nearly all the wharves about the harbor, but is not present on the yellow granite blocks of the wall of the east side to which we have already referred (plates XVII and III B). The vertical distribution of *Fucus* is also similar to that of *Ascophyllum*, except that the latter is dwarfed, much less abundant, and often quite wanting in the upper foot of the rockweed belt, which belt, above 5.5 feet, is dominated by *Fucus*. In the more exposed places the *Fucus* is usually quite unmixed with *Ascophyllum*.

Below the 5.5-foot line of the rockweed belt *Fucus* occurs commonly as isolated plants or in groups of 3 or 4 plants scattered among the *Ascophyllum*. Only occasionally is a patch of *Fucus* as much as 0.5 meter square found at these lower levels. Within the zone where both *Fucus* and *Ascophyllum* grow, the latter apparently conquers wherever its oöspores can find space to settle, and light enough to allow the young plants to start. The upper limit of *Fucus* moves upward on wooden wharves and on shaded stones or piles. On the wooden wharf at 2,230 north, on the west shore, the planks are not quite horizontal and the highest *Fucus* found is attached to the edges of these planks, at 6.75 feet, where water oozes out slowly after the fall of the tide below this level. It does

not grow on the faces of these planks above 6.25 or 6.5 feet. On the east wall of the wharf of the Research Laboratory, also at 1,100 north, the upper limit of *Fucus* is at 6.5 feet where exposed to the sun for the whole morning, but it goes up to 7 or even to 7.25 feet in the shade on the north sides of piles where protected from the sun and desiccation.

Fucus is prevented from occupying the very base of the walls of the wharf by the mud which would bury it, and perhaps also by the greater turbidity of the water at this lower stratum. *Fucus,* in general, is much less abundant in the lower third of the rockweed belt than in the upper two-thirds. It seems even less able than *Ascophyllum* to endure prolonged immersion in fresh water, as is shown by its distribution in relation to the fresh-water streams entering the harbor along the shore, or through the walls of the wharves. The only efficient competitor of *Fucus* on the wharf is *Ascophyllum,* which may shade out the *Fucus* or tear it off by the aid of a greater weight and toughness.

Interesting facts concerning the seasonal development of *Fucus* were suggested by its condition in April 1911. At this time the upper border of the band of *Fucus* was marked by a series of sporelings 1 to 3 cm. high, which were of a reddish-brown color, unlike the usual brown of *Fucus,* and shriveled up as if killed by frost. The *Fucus* plants on long stretches of the wall showed at this season not a single well-developed receptacle, where in summer dozens could be found. On some parts of this wall a few plants were seen with receptacles, but these were immature. It is evident from what is recorded above, of the condition of *Ascophyllum* in April, that the fruiting season of the latter is inaugurated much earlier than that of *Fucus.* Observations prolonged over the late fall and winter are needed to determine exactly the duration of these fruiting seasons.

Pylaiella littoralis robustus: This alga has been found in abundance on the wharves, only in April 1911. Its habitat was then the wharves of the west shore, especially the wharf of the Research Laboratory, between 2 and 3.5 feet. Several times during the summer it has been found in small tufts, always on the Research Laboratory wharf in shaded spots between the 3 and 4 foot levels, usually on the north end of the wharf, and more rarely in the shadow of piles on the east side. This alga has nearly always been found in summer in the Creek near 200 south. It is evidently favored by the low temperature of the water here, and by the protection from desiccation at low water.

Ralfsia clavata (Carm.) Crouan: This light or dark brown incrusting alga occurs on the piles and stones of wharves, especially of the west side of the harbor. It forms small, smooth, adherent disks each from 1 or 2 to 12 or 15 mm. in diameter, which, when old, have a slightly wavy outline. They are at first thin and tightly adherent but later become thick and more easily detached. This form is found in summer between the 2.5 and 5 foot levels, chiefly on the shaded sides of piles among young plants of *Fucus,* along the east and north faces of the wharf of the Research Laboratory. In April 1911, this species was far more abundant at one point than it has ever been in summer. Scores of young colonies 2 or 10 mm. in diameter were found on stakes near the wharf at 400 north by 170 west at 2.5 to 4 feet. The few observations made elsewhere in the harbor in April showed no unusual abundance of the alga, at this season, in any other location. *Ralfsia* is not found where subjected to flooding by fresh

water. It grows most abundantly where partially shaded, but it is apparently killed out by the denser shade of large masses of *Fucus* and *Ascophyllum* or even by tufts of *Bostrychia.*

RHODOPHYCEÆ.

The only red algæ found on the wharves are *Bostrychia rivularis, Delesseria leprieurii, Hildenbrandia prototypus,* and *Porphyra laciniata.* Their distribution is indicated on plate IX.

Bostrychia: The dense, wiry, blackish tufts of this alga reach a length of 2 or 3 cm. and stand so close together as to cover the surface for an area of several hundred square centimeters. It occurs on both wood and stone on all the wharves, of both sides of the harbor, in spots devoid of the rockweeds, though often more or less overhung by them. Its vertical range extends from about 2.5 to 6.5 feet. In shaded cracks of wet piles or dock logs *Bostrychia* has been found abundantly as high as 7 feet, and a few plants were found at 7.3 feet. This level is higher than that at which any other red alga occurs in Cold Spring Harbor or the neighboring parts of Long Island Sound. Aside from *Hildenbrandia* no other red alga occurs on the wharves or beach above the 4-foot level, which is the upper limit of *Porphyra.*

All the fruiting plants of *Bostrychia* found in summer bore tetraspores. In April 1911 and November 1912 the plants were of the same size and had as actively growing initials as in midsummer. The species is evidently perennial and seems not to be injured by freezing, even at its extremely exposed positions far above the mean low water level. It is evident from the tide-curves (plate XXIV) that *Bostrychia* at the 7.3-foot level must go without being wet by salt water for several days in succession during each series of neap tides. It might chance to be splashed by an occasional wave. Aside from the fact that at this height it must often be washed with rain there is no suggestion from the distribution of *Bostrychia* that it can endure immersion in fresh water. It has not been found close to fresh-water outlets, either in walls or on the natural shores.

Delesseria: This alga, though occasionally found in summer, on logs on the bottom, has not been seen on the wharves, except in September 1911, when it was unusually luxuriant. It flourished also at this time at a few points on the shore. It was found abundantly on piles and stones of the north end of the wharf of the Research Laboratory, between the 2 and 3 foot levels. The patches were here often several square centimeters in area and the plants 20 to 30 mm. high. Those that were fruiting showed only tetraspores. It is, of course, possible that this alga is more abundant in winter than in summer, though the brief examinations made in April and September did not show it to be at all common.

Hildenbrandia: This ubiquitous incrusting alga forms hundreds of red patches, often several centimeters in diameter, on the otherwise bare stones of the wharves. Such patches of *Hildenbrandia* we have already described (p. 31) on pebbles in the rivulets along shore. The lower limit of *Hildenbrandia* is at about mean low water and its upper limit, on the wharves and in the fresh-water rivulets, is at 6 or 6.5 feet, rarely at 7 feet. The vertical distribution of this alga is therefore as wide as that of the most widely distributed Schizophyceæ and Chlorophyceæ, like *Spirulina* or *Enteromorpha clathrata.*

It is probably limited in distribution upward by its inability to withstand desiccation or constant submergence in fresh water. Its lower limit is perhaps conditioned by the inadequacy of light and the certainty of being silted over at lower levels.

Porphyra: This alga is represented in summer by a few dozen small plants only. They are attached to stakes or to stones or piles of the wharves at, or just below, the 4-foot level. It was most frequently found on the wharf of the Research Laboratory, though it has also been seen on the east side at 950 south and between 1,700 and 2,500 north. An occasional plant may be seen on a stake or buoy in the middle of the harbor. In April 1911 we were surprised to find thousands of plants of *Porphyra* from 1 to 2 dm. broad on the pebbles of the bottom of the Inlet. Examination of the wharves at this time showed that *Porphyra* was little if any more abundant there than in mid-summer. We have already (p. 31) suggested the possible factors limiting the distribution of this alga.

4. THE UPPER LITTORAL BELT (FROM 6.5 TO 8 FEET).

The character of the shore in this belt differs markedly at different points about the harbor. On the Spit, and on parts of the east and west sides of the harbor, there is, at this level, a rather steep, well-drained, sandy or gravelly beach from 3 to 5 meters in width. At some points along the east and west sides and across the south end of the harbor this belt of the shore has a more gentle slope, a mucky soil, and is decidedly marshy. In the latter region especially there is a border 40 to 60 meters in width that is nearly flat. In spite of this marked difference in the character of the littoral region, many of the dominant plants found at these levels are shared in common by both the gravelly and marshy shores. Aside from those parts of the shore influenced by fresh water, the upper littoral beach and the upper littoral marsh have in common, also, many of the less abundant plants. Because so many of these plants may occur on any sort of substratum, we shall discuss the vegetation of the belt as a whole, though occasionally speaking of "beach" and "marsh" to distinguish a particular kind of substratum. For the sake of simplicity and clearness in presentation we will, however, discuss separately the seed plants and algæ of this belt.

A. SEED PLANTS OF THE UPPER LITTORAL BELT. (ASSOCIATIONS OF SPARTINA PATENS, SUÆDA, SALICORNIA, JUNCUS, OR SCIRPUS.)

The whole natural shore of the harbor for some distance below 6.5 feet is, as we have seen, completely dominated by a nearly continuous stand of a single grass, *Spartina glabra*. The only other seed plants found in that belt are *Lilæopsis* and a few stragglers from the belt above. Algæ of many species occur scattered through the *Spartina*, but, either because of their sparseness or of their small size, they are relatively inconspicuous.

In the belt we are now to discuss, that lying between the 6.5 and 8 foot levels, no such uniformity of the plant covering is found. The character of the vegetation here may differ greatly and sharply in immediately adjoining portions of the beach, where only very slight differences are apparent in the character of the substratum.

The dominant plant in any one portion of the upper littoral beach or marsh may be any one of eight species of seed plants. In some places there may be a

practically pure growth of a single one of these species, as is most often true of the grasses or *Juncus*. In other places the shore may be occupied by an association made up of two or three of these species. In a few regions the upper littoral beach is either entirely bare, in which case it may be either pebbly, sandy, or muddy in character, or it may bear close, blackish felts of minute algæ. The latter are most often found on the more stable, pebbly bottoms.

The eight species which, over larger or smaller areas, determine the character of the vegetation in this belt, are the following; they are mentioned in the order of their general prevalence: *Spartina patens, Suæda maritima, Salicornia europæa, Juncus Gerardi, Scirpus americanus, S. robustus, Distichlis spicata,* and *Salicornia ambigua.* Only nine other species have been recorded for this belt. Six of these nine species that may be nearly pure over small areas, or may be scattered among other species just above the *Spartina glabra* belt, are these: *Atriplex patula, Limonium carolinianum, Plantago decipiens, Scirpus nanus,* and *Triglochin maritima.* The other three species of seed plants that have occasionally been seen in this belt are *Atriplex arenaria, Iris versicolor,* and *Samolus floribundus.* Of these, the latter two are to be regarded as inwanderers, on wet shores, from the next higher belt. Their distribution is indicated in the list of plants and plant habitats at the end of this paper.

Each of the eight dominant species, except *Scirpus,* is distributed rather generally about the harbor, but the *Salicornias* and *Suæda* are represented by relatively few and scattered plants except on the Spit, while *Juncus gerardi* is nearly absent there, though abundant on the Marsh. *Scirpus americanus* and *S. robustus* occur only where fresh water is present on the upper littoral beach. These species are therefore entirely absent from the Spit. It is only rarely about this harbor that *Juncus gerardi* directly succeeds the *Spartina glabra,* as, *e. g.,* at 200 south by 1,150 east or at 550 south by 890 east. *Juncus* is usually separated from the *Spartina glabra* by a band of *S. patens.*

We may now discuss, in some detail, the general distribution and interrelations of the eight dominant species, and then attempt to discover the factors determining their distribution. Our treatment of those species occurring on the Marsh will be relatively brief, since this area has been closely studied and mapped in detail (plates XI, XXI, and XXII).

Spartina patens: This species, as was suggested in discussing the next lower belt, is most abundant on the estuarial marsh at the south end of the harbor, though present elsewhere, on parts of the upper littoral belt which have a gentle slope, and no fresh water flowing over them. The need of these conditions limit the development of a continuous zone of this plant chiefly to the northern and western portions of the Marsh, and to the western fourth of the south shore of the Spit. Elsewhere this grass occurs in narrow and short strips, chiefly between the 6.5 and 7.5-foot levels. We may illustrate the first type of area by describing in a general way the growth of *Spartina patens* on the Marsh and on the west end of the Spit; then we may note briefly the distribution of the narrow strips about the whole shore.

Spartina patens on the Marsh: This grass, growing in dense turfs, dominates nearly half the area of the estuarial marsh, east of the Creek, above the *Spartina glabra.* This area lies chiefly between the 6.5 and 8 foot levels, but at certain points on the Marsh this grass may get down as low as 5.5 feet (200 north by 1,020 east), while at other points it may run up nearly to the 9-foot level (100

south by 1,000 east and 200 south by 1,100 east). The lower margin of the *S. patens* belt is usually in contact with *S. glabra,* while at its upper margin it is succeeded over all this part of the Marsh by *Juncus Gerardi.* At one or two points considerable patches of *S. patens* are completely surrounded by the *Juncus* (150 to 300 south by 1,150 east). The large-scale map of the Marsh (plate XI) shows the relations of these two species there, and suggests a possible explanation of these islands of *S. patens* surrounded by *Juncus,* and of other peculiarities of its distribution (plate XIX A). It may suffice here to say that the islands referred to are really lower and wetter spots. It is apparently this greater saturation, rather than any difference in salinity, that enables the *S. patens* to crowd out the *Juncus* at these points. (See plate XI and fig. 3.) However, it must be remembered that the evaporation of the water left in these low spots at high tide would give rise to some concentration which would only be reduced by the leaching effect of heavy rains.

The competitors of *S. patens* on the Marsh which may form continuous stands of considerable area are, in addition to the *S. glabra* and *Juncus* just mentioned, *Distichlis, Scirpus americanus,* and *S. robustus.* The former is found in occasional patches not many square meters in extent, on several parts of the Marsh. (See plates XI and XXI.) The two species of *Scirpus* are more abundant at the upper levels of this belt, around the edges of the Marsh, where the soil water is nearly fresh. The region of contact of *S. patens* with each of these five species is not usually a line, but a rather broad band, in which the competing species are more or less intermingled. (See especially plates XI, XIX B, and fig. 3.)

Besides these mixtures of *S. patens* with other dominant species along the tension lines, there are several other species, scattered through the stands of this grass on the Marsh, the distribution of which will be indicated by Professor Conard. The most important of these species are: *Atriplex patula, Limonium carolinianum, Salicornia europæa, Scirpus nanus, Spergularia marina, Suæda maritima,* and *Triglochin maritima.*

Spartina patens, on the west end of the Spit: On the south shore of the Spit, from 590 to 1,000 west, *Spartina patens* forms a continuous band or belt, widening from 5 feet at its eastern end to 100 feet at its extreme western end (plate V). The general form of the area covered by it is indicated by the relative position of the 6-foot and 8-foot tide-lines on plate I. The lower limit of its distribution here is at 6.5 feet or slightly lower, the upper at 7.5 to 8.5 feet. The plants reach a height of 4 to 6 dm. to the top of the panicle, and form a close turf, with often 300 to 400 leaf-bearing shoots per square decimeter. The rhizomes and roots penetrate to a depth of 4 or 5 inches below the surface, and by their interweaving give rise to a very firm sod. All other plants are wanting, except an occasional plant of *Limonium* or *Suæda* or felts of algæ. The latter, of course, are confined to the surface of the soil between the *Spartina* stalks. *S. patens* in this region blooms freely, except near its upper and lower limits, beginning early in July and continuing till early September.

At its lower limit this grass sometimes stops abruptly against the *S. glabra,* and sometimes intermingles with the latter in a strip 1 or 2 feet in width (fig. 2). At other points along this shore *Suæda* or *Salicornia europæa* may be so abundant near the 6.5-foot level as to dominate an intermediate strip a foot or two in width between the *S. glabra* and the *S. patens.* But even in this intermediate strip numerous plants of *S. patens* and occasional ones of *S. glabra* are

present. It is only on the eastern half of the Spit that we find a nearly pure band of *Suæda* or *Salicornia* succeeding the *S. glabra* (plates v and xiv).

In the middle of the band of *S. patens* there are occasional more thinly covered areas where, in addition to the few dozens of *Limonium* or algal felts already mentioned, there may be scattered tufts, or now and then (as at 7.5 feet, 950 west) a patch several feet in diameter of *Distichlis*. Aside from these plants intruders are rare, the only others being isolated tufts of *Spartina glabra* or a few scattered plants of *Suæda* or *Salicornia europæa*.

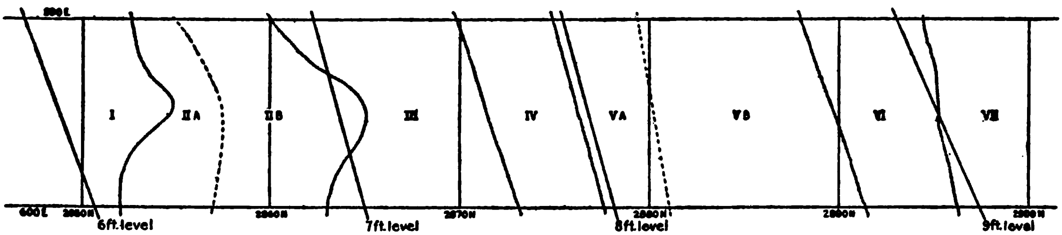


FIG. 2.—Zonation of South Beach of Sand Spit, Cold Spring Harbor, 590 to 600 East by 2,850 to 2,905 North, August, 1909. By H. S. CONARD.

Solid lines mark tide-levels; wavy lines mark boundaries of belts; dotted lines subdivide the belts.

I. *Spartina glabra*, 5 feet tall, in bloom at northern (shoreward) margin. Soil wet and muddy.

Boundary of I and II: A strip about 1 foot wide, with occasional plants of *Salicornia europæa* and *Suæda maritima* of tall stature, and *Spartina glabra* of normal size. Soil a wet sandy gravel.

II A. *Suæda maritima* dominant, with *Salicornia europæa* frequent and *Spartina glabra* occasional. There are patches of bare sandy gravel.

II B. Almost pure dense growth of *Salicornia europæa* and *S. ambigua*. Occasional plants of *Suæda maritima, Limonium carolinianum, Spartina glabra*, and *Spartina patens*.

III. Densely gregarious patches of *Spartina patens* and *Distichlis spicata*. Occasional plants of *Salicornia ambigua* and *Limonium carolinianum*. Soil a gravelly sand with humus.

Boundary of III and IV. *Spartina patens* ends abruptly. *Distichlis spicata* invades gravel by straight rhizomes. A strip about 1 foot wide of *Atriplex arenaria* and short and unhealthy *Suæda maritima*. Soil is gravel.

IV. Nearly bare sandy gravel. Very sparse scattering of *Atriplex arenaria* and *Suæda maritima*.

V. All fine sand with a few pebbles. A. *Suæda maritima* and *Atriplex arenaria* frequent; 3 plants of *Salicornia europæa*. B. Mostly bare sand; 1 *Salsola kali*, 1 *Suæda maritima*, 2 or 3 *Atriplex arenaria*.

VI. Sand. A few plants of *Cakile edentula* and *Solidago sempervirens*.

VII. Sand. *Solidago sempervirens, Cakile edentula, Asparagus officinalis. Ammophila arenaria* dominant.

Belts I and IV are continuous for a long distance. Between them the components of belts II and III may be distributed in almost any order.

The upper third of the belt of *S. patens* is rather more thinly covered with the grass. It has few felts of alga or plants of *Limonium*, and no *Distichlis* or *Salicornia*. It does contain a few plants of *Suæda*, of *Atriplex arenaria*, and *A. patula*. Only at the extreme upper edge do we begin to encounter wanderers from the upper levels of the beach. The commonest of these are *Ammophila, Panicum* sp., *Solidago sempervirens*, and *Cakile edentula*. Their frequency in the *Spartina patens* belt is indicated on Professor Conard's map of the cross-section of the Spit (plate xiv).

EXPLANATION OF PLATE XI.

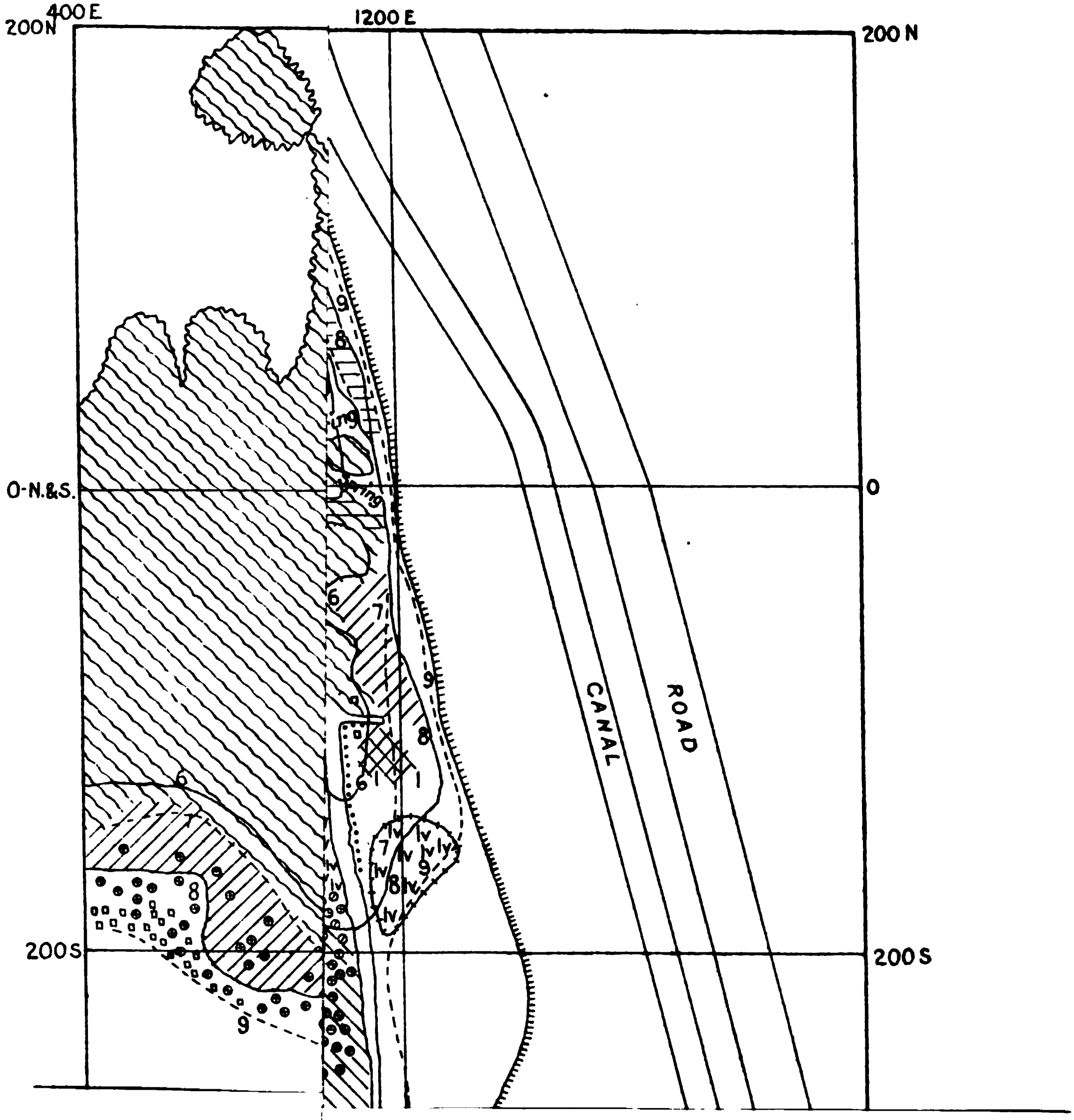
Composition of Vegetation in the Numbered Areas on the Map of the Æstuarial Marsh.

Area. Vegetation.

1. *Atriplex patula hastata.*
Iva oraria.
Scirpus americanus.
Solidago sempervirens.
Spartina glabra alternifolia.
Plantago maritima
2. *Gerardia maritima* } (equally scattered).
Triglochin maritima (dominant).
3. *Gerardia maritima* (dominant).
Limonium carolinianum (3 plants).
Spartina glabra alternifolia (2 doz.).
4. *Aster subulatus* (dominant).
Atriplex arenaria
Pluchea camphorata
Spartina glabra alternifolia } (equally interspersed).
Limonium carolinianum.
Solidago sempervirens.
Spergularia marina.
7. *Aster subulatus* (dominant).
Agrostis alba
Spergularia marina } (common).
Atriplex patula hastata
Plantago decipiens
Solidago sempervirens } (few).
8. *Agrostis alba* (dominant).
Aster subulatus (abundant).
Atriplex patula hastata (common).
Cyperus filiculmis (scattered).
Solidago sempervirens (common).
Spergularia marina (scattered).
9. *Aster subulatus* (dominant).
Plantago decipiens
Solidago sempervirens } (common).
10. *Spartina glabra alternifolia*
Spartina patens } (equally) (see fig. 21).
Aster subulatus (abundant).
Atriplex patula hastata
Salicornia europæa
Scirpus robustus
Solidago sempervirens } (common).
11. *Scirpus americanus.*
Spartina glabra alterniflora.
Spartina patens.
12. *Agrostis alba ?* (see fig. 21).
13. *Aster novæ belgii* (few).
Atriplex patula hastata.
Solidago sempervirens (abundant).
Spartina glabra alternifolia.
Spartina patens (dominant).
14. *Aster subulatus* (few) (see fig. 21).
Atriplex patula hastata (common).
Solidago sempervirens (few).
Spartina glabra alternifolia (common).
Spartina patens (dominant).
15. *Atriplex patula hastata*
Limonium carolinianum
Salicornia europæa } (common).
Scirpus nanus (abundant).
Spartina patens (common).
Spergularia marina (dominant).

Area. Vegetation.

16. *Aster subulatus* (common).
Aster tenuifolius.
Atriplex patula hastata (common).
Limonium carolinianum.
Spartina patens (common).
Spergularia marina (dominant).
17. *Scirpus nanus.*
Spergularia marina.
18. *Agrostis alba* (dominant).
Juncus Gerardi (common).
Solidago sempervirens.
19. *Agropyron repens.*
Ambrosia artemisiifolia (common).
Cuscuta sp.
Distichlis spicata.
Plantago major.
Polygonum sp.
Solidago sempervirens (dominant).
20. *Aster subulatus* (abundant).
Cyperus filiculmis.
Scirpus robustus (abundant).
Spartina glabra alternifolia (abundant near stream).
Spartina patens.
21. *Scirpus americanus*
Spartina glabra alternifolia } (equally dominant).
22. *Æthusa cynapium.*
Ambrosia artemisiifolia.
Aster subulatus.
Atriplex patula hastata.
Distichlis spicata (codominant).
Plantago major.
Scirpus americanus (codominant).
Solidago sempervirens.
Spartina glabra alternifolia.
Spartina patens.
23. General mixture of—
Agropyron repens.
Aster novæ belgii.
Carex silicea.
Erechtites hieracifolia.
Holcus lanatus.
Juncus Gerardi.
Lycopus virginicus.
Polygonum hastatum.
Ptilimnium capillaceum.
Scirpus americanus.
Scirpus robustus.
Solidago sempervirens.
25. A recently denuded spot:
Aster subulatus (dense stand).
Spartina glabra alternifolia (400 stalks).
26. A denuded area: *Aster subulatus.*
27. *Gerardia maritima* (abundant).
28. *Pluchea camphorata* (dense stand).


400 E
1200 E
200 N
200 N
0-N.&S.
0
200 S
200 S
CANAL
ROAD

The soil on which *S. patens* grows at the west end of the Spit is, at its lower margin, a compact, peat-like, saturated mud, having a depth of from 14 to 24 inches. At the upper margin the soil bearing the sparser stand of *S. patens* becomes drier, more sandy, and much thinner, often only 6 or 8 inches deep between the 7.5 and 8 foot levels.

Spartina patens on the steeper shores of the harbor: The short, narrow strips of *S. patens* found about the harbor are few and scattered on the east and west sides, but more numerous on the eastern half of the Spit. On the east side, for example, there are small patches of the grass on the wharf at 950 north, and still smaller ones, in which some *S. glabra* is found, on the elevated areas between the fresh-water streamlets on the east side of the Marsh, between 0 and 200 north (see plates XI and XIII). More considerable areas of nearly pure *S. patens* are found on the projecting points of the shore at 200 north and 300 north. On the west shore there are short strips of this grass at 790 to 930 north and at 1,010 to 1,040 north; a broad strip at 1,650 to 1,725 north; a short, narrow strip on elevated soil completely surrounded by *S. glabra,* at 1,750 to 1,765 north. Beyond this are found but two very small patches at 1,825 north and 2,000 north (plate XIII). The only stands of the grass on these two shores are at the points mentioned.

On the south shore of the Spit, as we have intimated above, the continuous band of *Spartina patens* found in the northwest corner of the harbor does not reach eastward beyond 590 west. East of this we find *S. patens* in isolated strips from 10 to 100 feet long. These strips of nearly pure *S. patens* may occupy the whole width of the upper littoral beach between the *S. glabra* and the 7.5-foot level, *e. g.,* at 280 to 390 east, 530 to 560 east, 675 to 730 east, and at 830 east. At other points, however (plate VII B), the *S. Patens* may form rather narrow and short patches of pure *S. patens,* very nearly surrounded by the *Suæda* or *Salicornia europæa,* which at these places form the dominant plants in the covering of the upper littoral beach, *e. g.,* at 250 west and at 430 to 450 west. At still other points the *Spartina* may occur scattered rather evenly through the dominant *Suæda* or *Salicornia europæa, e. g.,* at 370 to 480 west and at 390 to 530 east. (See plate V.)

The conditions affecting the distribution of *S. patens* are suggested by what we have said above of that distribution. It is evident that this grass can grow on either peat or mud, or even on sandy soil, between the 6 and 8 foot levels, if the soil is not flooded by salt water longer than 5 or 6 hours per day, and is not saturated by fresh water. How far each of these various factors works directly and how far indirectly has not been determined definitely in the only way it can be, namely, by experiment. It seems probable, however, from a study of the occurrence of this plant and its competitors, that it does not dominate on soils saturated by fresh water because it does not endure fresh water as well as its competitors, and therefore is driven out by them. That it will endure some fresh water in and above the soil seems evident from the fact that *S. patens* is found beside the fresh-water streamlets on the east side of the Marsh.

The lower limit of *S. patens* is probably determined chiefly by the competition of *S. glabra,* since in a few places where the latter is absent the *S. patens* goes down to the 6-foot level, and at 200 north on the east shore to the 5.5-foot level. Practically everywhere about the harbor *S. glabra* occupies the next lower belt, and it is evidently the unfavorable physical conditions for this latter

grass that keep it down to 6.5 feet and so determine the lower limit to which *Spartina patens* usually reaches. The upper limit of *S. patens* is probably determined by the physical character and salt-water content of the soil, both directly and by the competitors favored or excluded by these conditions.

The lateral boundaries of the patches of *Spartina* on the shore seem to be determined by the local characters of the soil. Thus, for example, gravelly sections of this upper littoral beach are pretty sure to be destitute of this grass, which is there replaced by *Salicornia, Suæda,* or *Atriplex.* Of course, it is possible that the coarser soil may be such in consequence of the lack of the *Spartina* as a binder. Wherever a fresh-water rivulet trickles across the upper littoral beach the band of *S. patens* is broken and *Scirpus americanus* pushes in to occupy the soil saturated with fresh water. Even *Spartina glabra* may, in these moist places, push above its usual upper limit, on knobs of peat that are high enough to avoid being constantly wet with the fresh water at low tide.

Juncus Gerardi: In the upper littoral belt this rush is found in dense turfs over very considerable areas of the Marsh (plate XX A), chiefly between the 7-foot and 8-foot levels, though sometimes higher, as will be seen from the work of Professor Conard (plates XI, XXI, and XXII). Elsewhere about the harbor only two patches of it are found, and these are small in area and the shoots of *Juncus* are intermingled with those of other species, oftenest with those of *Spartina patens.* In one of these areas (200 north by 1,060 east at 7.5 to 8.25 feet), the patch of *Juncus* is 0.5 meter wide and 4 meters long. There is here a sparse admixture of *Solidago sempervirens* and *Scirpus americanus.* On the west shore (1,700 north at the 8-foot level) there is a dense turf of this *Juncus,* of 2 square meters area, the only one on the whole west side. On the Spit this rush has not been seen at all.

The distribution of this *Juncus* can evidently be studied best on the Marsh and will therefore be left for Professor Conard to discuss. We may simply remark at this point that the deep, peaty soil inhabited by this species is practically wanting, except on the Marsh. (See plates XI, XXI, and XXII, and fig. 3, p. 111.) It is also interesting to note that at the one point on the west side where this rush occurs it is accompanied by the two plants usually associated with it on the Marsh, *Distichlis* and *Spartina patens.* The soil on which these three species here find congenial conditions is a deep, peaty muck like that of the Marsh, which is formed chiefly by the sedimentary deposits from the very considerable stream that enters this side of the harbor at 1,650 north.

Suæda maritima in the upper littoral belt: This low, glaucous annual is distributed abundantly along the south shore of the Spit (plates IV A, V, VII B, and XIV), and occurs in rather frequent smaller patches on well-drained portions of the Marsh, but is rarely found on the east or west sides. On the Spit *Suæda* is distributed pretty generally from end to end, chiefly between the 6.5 and 7.5 foot levels, though it occasionally gets down to the 6.25 or up to 8 foot levels. In some stretches of the upper littoral beach it is the dominant species in the belt immediately above the *Spartina glabra.* On other parts of this beach *Suæda* may be crowded downward into the *S. glabra* or upward toward the 8-foot level, or occasionally be crowded out altogether, by such competitors as *Spartina patens, Salicornia europæa,* or *Distichlis spicata,* which are the other species that may become dominant in this belt. In still other portions of this belt *Suæda* may occur as a mere sprinkling over areas dominated by one of the three species

just mentioned, *e. g.*, on the Spit from 480 to 590 west. Of course, the distribution of an annual species like this may differ somewhat from year to year, but not very widely, since seedlings each year can find suitable space only in the areas occupied in the preceding year by their parents or by their, likewise annual, competitor, *Salicornia europæa.* The only chance *Suæda* has of invading the more considerable area occupied by its perennial competitors, *Spartina patens, Distichlis,* and *Salicornia ambigua,* is when these are smothered out by flood-trash, or uprooted by fishermen digging on the beach. Such free soil is usually promptly appropriated by either *Suæda* or the annual species of *Salicornia.* In those areas on the Spit where *Suæda* is the dominant species (*e. g.*, 780 to 820 east, 20 east to 380 west and 480 to 590 west), the band of this plant may be from 8 to 12 feet wide. In these stretches the *Suæda* may be 2 or 3 dm. high and stand as thickly as 100 to 200 plants per square meter. In such areas there may be only 2 or 3 plants per meter of *Atriplex arenaria* or *Limonium*, or 5 to 10 plants of *Salicorna europæa,* to dispute its dominance. From 20 east to 200 east at 6.5 to 7 feet it nearly equals in quantity the barely dominant *Salicornia europæa,* while between 7 and 8 feet it becomes much sparser than the latter (plates XIII and XIV). In other areas, *e. g.*, from 20 to 270 east, we find a dozen or two plants of *Suæda* per square meter, scattered through the dominant *Salicornia europæa* or *S. ambigua.* Even in this strip there are short stretches where the *Suæda* is entirely crowded out by these competitors, except at the very upper and lower edges of the upper littoral belt. Toward the west end of the Spit (800 to 1,000 west), *Suæda,* often to the number of 8 or 10 plants per square meter, is scattered, along with occasional plants of *Salicornia europæa, Limonium,* and *Atriplex patula,* through the dominant *Spartina Patens.*

Suæda on the Marsh: On the Marsh south of the harbor *Suæda* is found most abundantly on the better-drained parts, such as the edges of ditches or along the tide-streams (*e. g.*, 20 north to 30 south by 950 east and 100 south by 1,090 east). Nowhere on the Marsh, however, does *Suæda* attain the maximum size or density of stand found on the Spit.

On the west shore *Suæda* has not been seen at all, and on the east side it has been found only on the stone pier at 950 north, where it is usually scarce.

From the examples cited above, which illustrate the more typical areas that have been occupied by *Suæda* during the time our work has been in progress, it will be seen that it may grow under the following conditions: It is found on well-drained, peaty soil (*e. g.*, on the Marsh), or on relatively thin layers of fine-grained mud overlying sand or gravel (*e. g.*, at the upper edge of the *Spartina glabra* on the Spit). Its densest stands, however, are found on the higher levels of the upper littoral beach, where the soil is a pretty clear sand or fine gravel. Those parts of this beach on the Spit where *Suæda* occurs over its whole width have a sandy or gravelly soil down to the very edge of the *Spartina glabra.* *Suæda* always grows in well-lighted areas, with no more shade than that furnished by the small, scattered plants of the *Spartina glabra* at the upper edge of its belt.

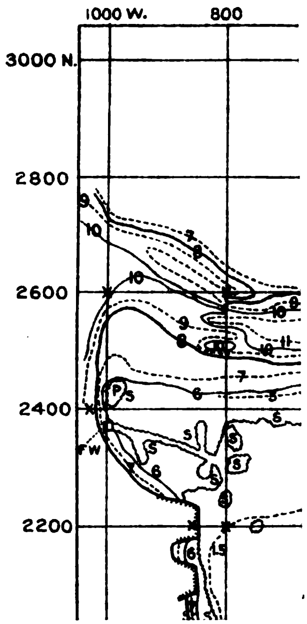
Suæda is not found at any station about the harbor where fresh water is present in the soil, or covers the soil, or surrounds the shoot of the plant at any stage of the tide. There is no experimental evidence to show what amount of exposure to salt water and to air *Suæda* will endure. The fact that it occurs

at the 6.5-foot and in a few cases at the 6-foot level shows that it can withstand a submergence of 3 to 3.5 hours per tide, or 6 or 7 hours per day. Its occurrence at the 7.5 foot and, more rarely even at the 8.25-foot level, where the shoot may not be submerged for several days together, shows likewise that frequent submergence of the shoot is not necessary, even in regions with a rather dry atmosphere, like the Spit. The plants of *Suæda* are, however, rarely so high on the beach that their roots can not reach to a soil that at least part of the time is saturated with salt water. It is to be recalled here that, as one can see on any calm day on the beach, the tide-water is carried up several inches above high-tide level by capillarity. This means that the water goes considerably higher in the soil than the 7 or 7.5-foot level at high water of a neap tide. That this level of the soil-water is a factor of some importance to the *Suæda* is indicated by the fact that, *e. g.*, at 800 to 900 east on the Spit, this species stops near the 8-foot line, leaving a beach above this that is quite bare of vegetation. In this place there are no discoverable differences in the soil above and below the 8-foot level, and there are no plant competitors above this contour. It seems probable, therefore, that the lack of sufficient soil-water may be the condition excluding *Suæda* from the upper levels of this shore. Unfortunately no actual determinations of the water-level or of the salt-content of the soil-water have as yet been made at this point.

On some parts of the upper littoral beach, as has been noted above, the *Suæda* is displaced from levels between 6.5 and 7.5 feet by *Distichlis* or *Salicornia europæa*. Whether the competition between these plants is such that some slight local difference in the character of the soil may give one or the other of these two species the advantage over the *Suæda* is uncertain. It is possible that the greater amount of humus usually present in the soils occupied by these two competitors may allow them to become established in these areas, while in the more purely sandy soil *Suæda* is the successful competitor.

Salicornia europæa in the upper littoral belt: This plant is found abundantly on the Spit, often in dense stands for from 5 to 20 meters along the shore. It is widely but sparsely scattered over certain parts of the Marsh also, while it is wanting from the other two sides of the harbor, except for two points on the eastern shore. (See plates V, XA, XIII, and XIV.)

On the south shore of the Spit this species of *Salicornia* reaches its maximum development in size and abundance as well as in purity and density of stand. At the western end of the Spit (980 to 1,000 west), this *Salicornia* was found scattered thickly through a belt of dwarfish *Spartina glabra* some 4 or 5 meters wide, near the upper border of the latter. Near the 7-foot level *Salicornia* is mingled with *Spartina patens*, also with some *Distichlis* and *Suæda*, while at the 7.5-foot level *Salicornia* becomes completely dominant. Farther eastward the sprinkling of *Salicornia* becomes more copious, *e. g.*, though this upper littoral belt from 480 to 590 west was dominated by *Suæda*, there was an admixture of nearly as many plants of the *Salicornia*. Between 380 and 480 west this belt is dominated by *Salicornia europæa*, except for an occasional narrow bar of *Spartina patens* cutting across it. Between 200 and 380 west this *Salicornia* is usually very sparsely represented, but from 200 west to 20 east it is, in most years, exceeded in numbers only by *Suæda*. Eastward from the latter point *Salicornia* dominates this upper littoral beach as far as 280 east, though often mixed with abundant *Suæda*. Next follows a stretch dominated by



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Spartina patens, but from 480 east on to the east end of the Spit this belt is dominated by *Salicornia europæa,* often mixed with numerous bushy plants of its relative, *S. ambigua.* In one place only (620 to 660 east), does the latter become abundant enough to really crowd out the more erectly growing *S. europæa.* Three or four similar interruptions of the band of *Salicornia europæa* near the eastern end of the Spit are due to short patches of *Spartina patens* or *Distichlis.* At the eastern extremity of the Spit, *Suæda* and *Atriplex patula* may be mingled with the *Salicornia,* while at the very tip the *Salicornia* is usually sprinkled thinly over an otherwise comparatively bare sand beach (plates v and xiii).

On the Marsh *Salicornia europæa* may in some places be sparsely distributed and in other parts areas of several square meters may be covered to a density of 100 plants per square decimeter. Throughout the Marsh it is chiefly confined to the margins of the tide-streams, tide-pools, and artificial ditches (100 north by 1,150 east at 6.5 to 7.5 feet and 100 south by 900 east). On spots made bare by the smothering out of *Spartina patens* by tide-trash, *Salicornia europæa* is often the first thing to appear when this trash is finally removed by some very high tide, *e. g.,* at 100 north by 1,090 east in 1909. On locally elevated areas in the midst of the *Spartina glabra,* even down to the 6-foot level, *Salicornia* is sparingly mixed with such species as *Aster subulatus, Atriplex patula, Limonium carolinianum,* and *Scirpus nanus,* as, *e. g.,* at 400 to 440 south by 770 east, between two streams.

On the east shore of the harbor *Salicornia europæa* is usually seen only at 200 north, between 6 and 7.5 feet, where it is only sparsely sprinkled among the *Spartina glabra* and the *S. patens* on this rather well-drained point of the shore. In one season only (1908) were a few scores of this plant found between 7.25 and 7.75 foot levels, on the stone pier at 950 north. Not a single plant of this species could be found along the whole west shore, from the northern edge of the Marsh to the Spit, though a careful search was made for it.

The factors influencing the distribution of this species may best be suggested after noting the distribution of the second species of *Salicornia,* which immediately follows.

Salicornia ambigua in the upper littoral belt: This perennial, half-evergreen species of *Salicornia* is confined to the eastern third of the Spit, except for a colony of 5 tufts, each 0.5 meter across, that has established itself on the north side of the stone pier on the east side, and a single plant at 1,010 north on the same shore. Mature, established plants are readily distinguished from those of *S. europæa,* but it is possible that this species may be represented on the Marsh by seedlings or young plants which were not distinguished from those of the annual species. On the south shore of the Spit *S. ambigua* is chiefly confined to the region between 390 and 600 east (plate xiii), not more than a score of plants of this form being found outside these limits. Only between 620 and 660 east, however, does this *Salicornia* become completely dominant. Here it forms a practically pure stand, with thickly matted branches, over a strip 1.5 meters in width, between the 6.25 and 6.75 foot levels (plate x b). Along the beach from 390 to 620 east this species is mingled with or at times crowded out by *S. europæa,* with now and then a turf of *Spartina patens* or *Distichlis* to interrupt the continuity of the stand of these two glassworts. Beyond 660 east the plants of *S. ambigua* are either scattered singly or may be grouped in twos and

threes, over a beach covered chiefly, though often sparsely, by either *Suæda* or *Salicornia europæa*. There is one group of a dozen of these perennial *Salicornias* between 790 and 820 east, of which most are 6 or 8 dm. across the individual plant (plates II and XIII).

The distribution of the two species of *Salicornia:* From what has been said above of the distribution of these two *Salicornias,* it is evident that the concurrence, in any area, of all the conditions allowing the establishment of a dense stand of either is rather rare on the shores of this harbor. Even the thinner stands occur in but a few and relatively small areas, except on the Spit. We are unable to do more than *suggest* the possible factors influencing the horizontal distribution along the shore. We have been unable to discover any very probable determinant of the vertical distribution of these two plants. It seems evident that the horizonal extent of the patches of the annual *S. europæa,* along the beach, is determined by its perennial competitors, especially by *Spartina patens* and *Distichlis.* The seedlings of this *Salicornia* can start only on unoccupied soil, which means either soil that has been bared of its competitors or soil that can not be successfully occupied by them, even with their advantageous habit of spreading to adjoining territory by means of their rhizomes. It will be interesting to note in this connection that in early April 1911, when the beach was still bare of vegetation after the winter, many seedlings of *Salicornia,* probably *S. europæa,* were found on the Spit far beyond the areas that are occupied by mature plants in summer. Many of them, for example, were found on the mud between the dead stumps of the *Spartina glabra,* down as far even as the 5-foot level. Others had started higher up, where they would be sure, later on, to be shaded out by the rapidly growing shoots of *Spartina patens.*

Shreve, and also Chrysler (Plant Life of Maryland, p. 131 and p. 178), have suggested that *Salicornia europæa* grows on areas where the soil-water is subject to concentration by evaporation, and that the high salinity so attained is really the factor that determines the occurrence of *Salicornia* on these areas. This assumption would not adequately explain the distribution of this species at Cold Spring Harbor, for here, as we have seen, it grows luxuriantly on beaches the soil of which is flushed out by a submergence of from 3 to 3.5 hours each tide. Moreover, *S. europæa* grows on the point between two streams, at 440 south by 770 east, just above the 6-foot level, where it must be overflowed by fresh water for at least 3 or 4 hours daily. As the tide rises the fresh water of the two streams is backed up north of the causeway, and it is not until the tide has risen to at least a foot above the substratum that the layer of fresh water next the substratum is replaced by salt water. Salinity tests made at this point show specific gravities of soil water of from 1.015 to 1.017. It is to be remarked, however, that *Salicornia* has never been found growing where fresh water is constantly present in the soil or flowing over it at low tide.

The *Salicornias,* at least *S. europæa,* grow on either muddy, sandy, or gravelly soil, though the denser stands of both species are found on the gravel. All soils bearing either *Salicornia* have at least moderately good drainage, for example, when growing near tide-pools it is always on the more elevated parts of their margins, above the constant water-level. *Salicornia* is found in well-lighted areas, in the open sunlight, except for the little shade given it in some places by the neighboring *Spartina glabra.* Neither *Salicornia* has been seen on the west side, where the conditions are apparently otherwise favorable, but where, as we have seen, these levels of the beach are deeply shaded for half the day.

The seedlings of *Salicornia europæa* are very numerous in the spring. In July each year plants of all sizes are found, from seedlings of 2 or 3 cm. up to mature plants. This indicates a marked difference either in time of germination or in rate of development, for no seeds have as yet been shed even from the oldest plants of the season. The perennial *S. ambigua* does not appear to spread by the rooting of its decumbent branches, and probably does so by its seeds, though its seedlings were not distinguished from those of *S. europæa.*

The vertical range of distribution of *Salicornia europæa* is from 6.5 to 7.25 feet, but small plants of it have been found as low as 5.5 feet (200 north by 1,020 east), and rarely it goes up to 7.75 feet (2,860 north by 500 east and 100 south by 900 east). *Salicornia ambigua* is found only between the 6.5 and 7 foot levels on the Spit, but may be capable of ranging much more widely where conditions encourage a more abundant growth. As a general conclusion from all observations made on these *Salicornias,* it may be suggested that the vertical distribution of these plants is determined primarily by physical conditions, of which the chief are the time of submergence of the shoot at its lower limit and the low percentage of soil-water at its upper limit. The horizontal distribution is directly influenced somewhat by soil characters, but is apparently determined ultimately, in the case of *S. europæa* at least, by the power of its perennial competitors to hold their own against the seedlings of the *Salicornia.* Between the two species themselves there is evidently keen competition.

Scirpus americanus in the upper litoral belt: This plant, which is a dark-green, few-leafed rush with triangular culms, about 0.5 cm. thick, and from 0.5 to 1 meter high, is widely scattered about the harbor in this belt, except on the Spit (plate XII). Along most of the east and west shores where this rush occurs at all it is sprinkled in with *Spartina glabra* near the upper border of the latter (plate IV B). Higher up there is still but a sprinkling among the successors of the *Spartina,* such as *Spartina patens* (*e. g.,* 1,000 to 1,020 north by 1,050 east). In still other places, though the stalks of the *Scirpus* may be thinly scattered, the soil between them may be destitute of other plants and perhaps covered with a layer of tide-trash beneath which this plant seems to persist more readily than other species. There are but few places along the west shore where this *Scirpus* is abundant enough to dominate the upper littoral belt (*e. g.,* between 640 and 800 north, 900 and 1,000 north, 1,850 and 1,900 north). Only on the southern end of the Marsh at the head of the harbor (350 to 500 south by 1,000 to 1,150 east) do we find this species really dominant over any considerable area (plates XV B, XIX B, and XX A). Even here it seldom occurs in as pure a stand as that formed by *Spartina glabra, S. patens,* or even by *Suæda* and the *Salicornias* on the Spit. The soil occupied chiefly by *Scirpus* is usually firmly bound by its rhizomes, which run about horizontally about 10 to 15 cm. below the surface. In the denser stands there are 10 to 15 culms per square decimeter.

The soil bearing *Scirpus americanus* is peat or mud, chiefly between the 6 and 8 foot levels. Sometimes, near the larger rivulets, it gets down to the 5-foot level on lumps of peaty mud which are surrounded by fresh water for 4 or 5 hours at each low tide (1,250 north, on the west shore). It does not grow on the gravelly areas from which this peaty top-soil has been eroded by these streamlets. On the other hand, this rush may grow at considerably higher levels than the upper limit mentioned above. This is true at one or two points along the west shore (*e. g.,* 1,700 north), and especially on the marshy area

south of the harbor, where, as noted above, this species attains its best development. Here it grows densely on soil at the 8.5 or 9 foot level, and at one place it is found at 9.25 feet. On the sunny east shore at 1,000 and 1,040 north this rush forms rather dense patches near the 8-foot level, and ascends still higher near the inflowing fresh-water rivulets.

In the preceding paragraph reference is made to the occurrence of this *Scirpus* near fresh-water streams, and to its complete absence from the Spit, which is devoid of fresh water. After studying the entire shore of the harbor, it is clear that *Scirpus americanus* is found only in soils where fresh water is present, either running over the surface or barely saturating the mud as the water seeps through from little springs in the underlying gravel. This latter seems to be the case, for example, on the west shore, near 800 north, 1,800 north, and 1,900 north, where, though no fresh water is found running over the beach between the 7 and 8 foot levels when the tide is out, yet the soil is constantly saturated even after many hours exposure. Moreover, the water collected in holes dug in this soil is entirely fresh to the taste and, at low tide, fresh water is also found trickling out of the beach at the 3 and 4 foot levels, directly below these *Scirpus* areas. On the Marsh also this *Scirpus* often grows in spots where no fresh water is visible on the surface. The soil-water, however, proves to be fresh when its specific gravity is taken. This is true, for example, of the large area between 400 and 500 south and 900 and 1,100 east, which is dominated by *S. americanus*. The soil-water here is practically fresh during the growing season, except just after the very high storm-tides mentioned above.

In brief summary of the conditions under which *Scirpus americanus* grows, we find that it is a plant of sunny situations. It is absent from shaded soil on the west side, though this be wet. In fact, the *Spartina glabra* from the belt below has been found to replace this rush in such wet, shady spots (see p. 45). *Scirpus* grows chiefly on soil between the 6-foot and 8-foot tide levels, except on the Marsh and at one or two spots on the east side, where it may reach the 9-foot level in wet, sunny places. This gives the plants an exposure of 15 or 16 hours per day in the case of the lower ones and of 24 hours per day for the higher ones, except on the 5 or 6 days of each month when high spring or storm tides occur. The submergence varies from 3 to 10 hours per day.

The critical factor determining the lower limit of this *Scirpus* is probably the high salt-content of the soil. It never gets far below the 7-foot level, except where fresh water is abundant enough to wash the salt out of the soil. It is, of course, possible that this fresh water really acts indirectly, by preventing the growth of its competitors in these soils (*e. g.*, of *Spartina glabra*). It is conceivable, for example, that this *Scirpus* might occupy any soil between the 5.5 and 8 foot levels, if only its competitors are kept out. This has not as yet been experimentally proven.[a] The upper limit of distribution is probably determined by shade, or by the lack of sufficient soil-water on some parts of the beach. Elsewhere, on the contrary, even in wet soils, its upper limit seems fixed by the competition of other species which can not follow the *Scirpus* down to levels that are flooded by salt water, but can successfully compete with it when they have not this adverse condition to meet.

Scirpus robustus on the upper littoral beach: This large, more leafy rush resembles *S. americanus* in its distribution, but is less abundant and less widely

[a] Tests made at a few points show that this species can grow in soil water with a specific gravity of 1.006 or even of 1.017.

distributed (plates XI and XII). There are but four patches of it on the west side and only six on the Marsh, and it is entirely wanting from the east side, north of the Marsh, and from the Spit. This species of *Scirpus* is, in fact, less abundant and less widely distributed than several of the other plants of this belt to be mentioned later. It is discussed here, immediately after *S. americanus*, for the sake of more ready comparison with this species. *S. robustus* is confined, like its relative, to areas with fresh soil-water. It rarely forms pure stands of any considerable extent. Stands of 50 square meters are found at 1,600 north on the west side, and one near 500 south by 880 east. Nearly pure stands of smaller area are present at 590 south by 740 east and near 120 south by 1,200 east. More often it is mingled with *Spartina glabra*, *S. patens*, or *Scirpus americanus*; *e. g.*, on the west shore at 1,980 to 2,020 north or on the Marsh at 550 south by 730 east. The lowest level from which this species has been recorded is 7 feet and its upper limit is at 9 or 9.25 feet. As was suggested above, this *Scirpus* is found only on soils supplied with fresh water. In some areas this water is evident on the surface, *e. g.*, on the west side at 1,415 north, on the Marsh at 120 south by 1,200 east. In other places the fresh water is not at first evident, but is found on investigation to be present in the soil. A striking instance of the latter sort is the small area, between two streams at 470 south by 830 east, which is elevated 1.5 or 2 feet above the bed of these streams. This area is covered with a mixture of *Spartina glabra*, *S. patens*, *Scirpus americanus*, and, most prominent of all, the present species. This same mixture extends eastward from the point named on soil, from 8 or 10 inches below the surface, of which a rivulet of fresh water trickles out at low tide. Not only is the soil-water fresh, but the overlying water at high tide never becomes very salt. Specific-gravity tests made at this point when the tide was at the 8-foot level showed a density of but 1.005 at the surface of the soil bearing these plants. At the time of the spring tides, which in summer reach 9 feet, or of storm tides, which in summer reach 10 feet and in winter even 12 feet, all inflowing fresh water must be backed up south of the road embankment, which crosses the Creek. The whole Marsh would then be covered with from 1 to 3 feet of sea-water with a density of 1.019, like that of the harbor itself. This shows that the shoots and more superficial roots and rhizomes of this plant can endure submergence in salt water for several hours a day, even when in a growing condition. It is probable, however, that the salt water never penetrates far into the soil here, because of its compactness and of the constant supply of fresh water from below.

Distichlis spicata on the upper littoral belt: This is a slender grass 4 or 5 dm. in height, with narrow, often glaucous leaves. It grows, chiefly between the 6.5 and 7.5 foot tide-lines, in a number of small areas on the Spit, at a few points on the Marsh, at one point on the east side, and two on the west shore (plates V, XIII, and XIV). Pure, or nearly pure, stands of *Distichlis* are found at a few points on the Spit (plate XX B). These are but a few meters long each, but 6 or 8 dm. wide, and all are near the 7-foot tide level (*e. g.*, 500 east at 7.75 feet, 580 to 590 east at 6.5 to 7.5 feet, and 800 to 820 east at 6.5 to 7.5 feet). On the Marsh similar dense growths of *Distichlis*, over smaller areas, are found at 0 north by 940 east at the 7.25-foot level, and at 370 south by 820 east near 7.5 feet. Elsewhere about the harbor *Distichlis* is mingled with *Spartina patens*, as at several points on the Spit (950 east, 800 to 1,000 west), on the

west shore (800 to 930 north, 1,600 north), on the east side on the pier (950 north), and finally on several small areas of the Marsh (*e. g.,* 0 south by 1,200 east). In other areas where *Distichlis* is still dominant, there may be a large admixture of *Suæda* or *Salicornia,* or even a scattering of *Atriplex arenaria* (*e. g.,* 2,700 north by 0 east, 2,850 north by 800 east).

The soil on which *Distichlis* grows is a partially drained, peaty muck, occasionally mixed with sand, as, for example, at the western end of the Spit. More rarely this grass is found in comparatively fine sand, in which on the Spit (750 east) it gets up above the 8-foot level. Nowhere about this harbor was *Distichlis* found growing in the shade or in soil wet with fresh water. The latter fact may, of course, indicate that the fresh water is directly injurious, or perhaps we should say that the semidiurnal alternation of fresh and salt water is unendurable. Or on the other hand, its absence from wet areas may mean that it meets other competitors, or meets some of its usual competitors at a greater disadvantage on wet soils. This grass lives on soils of quite varied character, taking all sides of the harbor into account, which indicates that it could occupy many other areas than at present if it were not for its competitors. In fact, then, it seems clear that the chief influence determining the limits of the *Distichlis* in a horizontal direction along the beach is the competition of its neighbors.

It is difficult to discover what external condition fixes the lower limit of *Distichlis* at 6.5 feet. It may be that the shoot will not endure a submergence of more than 2 or 3 hours each tide or that the rhizome can not withstand submergence longer than 3 or 4 hours per tide. On the other hand, it may well be that it can not compete successfully with *Spartina glabra,* with which it is nearly always in contact at its lower margin. The upper limit of this grass is quite variable, but it has proven impossible to determine whether this is fixed directly by some character of the soil, such as the water-content, or by the competing plants there present.

It is, of course, realized, as has been mentioned in other cases, that the particular conditions which limit the distribution of any species can not be determined by field observation alone, but that resort to experimental study will be necessary to do this with certainty. At the start, however, field observation must be relied on to indicate the possible factors from among which the experimenter may hope to select the actual controlling factor or factors. The suggestions offered in connection with most species in this paper are not made in the belief that they are finally established as causes of the distribution found, but as suggestions likely to prove useful to the experimental investigator.

The distribution of the nine other species of angiosperms found in this belt, but which seldom dominate any area above a few square decimeters in extent, may now be briefly indicated, taking them up in alphabetical order.

Atriplex arenaria: This hoary-leafed annual is found very sparsely scattered on the eastern half of the Spit (plates v and xiv), on the Marsh (plates xi and xiii), and on the old pier at 950 north on the east shore. Its usual range is from the 7-foot to the 8-foot levels, though its extreme range is from 6.25 to 8.75 feet. It occurs in rather sandy soil on the Spit, but is most frequent in the turf of *Spartina patens* along the edges of the tide-streams and ditches on the Marsh.

Atriplex patula hastata is, in most years, very much more abundant than *A. arenaria.* It is also more widely distributed about the harbor and has a greater vertical range (plates v, xi, and xiii). This species has been recorded on the

east side of the harbor at 320 north (about 10 clumps, in 1912), and at 400 to 480 north whenever fresh water is absent. The densest group about the harbor was found on the pier at 950 north by 970 east, where there were 150 plants in 1912. On the south side of the harbor this plant is usually distributed rather sparsely over most of the area of the Marsh. It grows here chiefly between the 7-foot and 8.25-foot tide-levels, is most frequently associated with *Spartina patens,* and is oftenest found on the better-drained soil at the edges of tide-pools, streams, or ditches. Its general frequency is that indicated on the area mapped in plate VII. On the west side this species is sparsely but widely distributed along the whole natural shore (740 north, 1,200 to 1,410 north, 1,650 to 1,750 north and 1,970 to 2,070 north). Usually it is found among *Spartina patens,* but it is sometimes mingled with *Solidago sempervirens* near the 8-foot level, and it is absent from soils saturated with fresh water. On the south side of the Spit, *Atriplex patula* has the same wide but sparse distribution that we have noted elsewhere. It is found scattered in the dense turfs of *S. patens* (800 to 1,000 west), or close to the upper margin of *S. glabra* (840 east at 6.5 feet). The more usual range of this *Atriplex* is from 6.5 to 7.5 feet, but at 400 to 480 north on the eastern shore it gets down below 6 feet, while on the well-drained shore at 320 north on the east side, it goes above 8 feet. On the west shore, near 1,800 north, and on the north shore of the Spit, between 400 east and 400 west, it is often found at 8.5 feet.

Iris versicolor, while really to be regarded as a denizen of the next higher belt, may form dense clumps of vigorous, abundantly fruiting plants in the upper littoral belt, on firm soil that is protected by neighboring springs and rivulets from saturation by salt water (plates IV B and XII). Thus, on the west shore (1,350 north, 1,400 north) *Iris* gets down to 8 feet or just below, while on the east shore it grows in soil at 7.5 feet, or even, at one point, at 7 feet. In the latter locality (10 north by 1,192 east) the soil-water at this level, and the sap of the *Iris* roots growing in it, are not at all salt to the taste. The soil, however, is covered with salt water twice daily, except during two or three neap tides of each fortnight. *Iris* forms a very striking example of the way in which the shoots of some inland plants can withstand immersion in salt water, if only the soil-water be fresh. The general occurrence of this species about the harbor is indicated on plate XII and will be discussed in speaking of the vegetation of the next higher belt.

Limonium carolinianum is one of the most widely distributed species of this upper littoral belt in soils free from the influence of fresh water. This has often been suggested above in speaking incidentally of its occurrence in stands of other species. It is a broad-leafed, thick-rooted perennial found on all four sides of the harbor. On the east side there is a bare sprinkling of it in the better-drained spots from 20 to 450 north and from 960 to 1,150 north, while between 800 and 900 north, at 7.75 to 8 feet, there were 30 plants in 1912. Finally, on the pier at 950 north, is found the densest and most extensive stand about the harbor. There are over 300 plants around the border of this wharf, and where densest there are 20 plants per square meter.

On the Marsh, *Limonium* occurs chiefly along the northern border between 6.5 and 7 feet, usually bordering tide-pools, tide-streams, and ditches (0 north by 880 east), and also on certain artificial, gravelly elevations (10 south by 800 east). The total number of plants on the Marsh is not over 150 or 200,

and the general scattered distribution of the plant is indicated by that shown for a typical area on plate VII B.

On the west shore *Limonium* has been found at only three points, all of which are artificially gravelly areas. A few plants are at 750 north, on a dilapidated boat-landing. About a dozen specimens were found at 1,070 north and the same number at 2,090 north.

At the Spit, *Limonium* is most abundant on the western quarter of the south shore (plates V, X B, XIII, and XIV). In the broad band of *Spartina patens* here between 700 and 900 north several dozens of this species are scattered, sometimes 4 or 5 in a square meter. On the eastern half of the Spit, *Limonium* is scattered very sparsely; *e. g.*, only 10 plants were found between 0 and 260 east. Beyond this, eastward to 840 east, the plants may be locally somewhat more abundant, but on the whole they are evenly scattered, and not more than 100 plants are present altogether on this half.

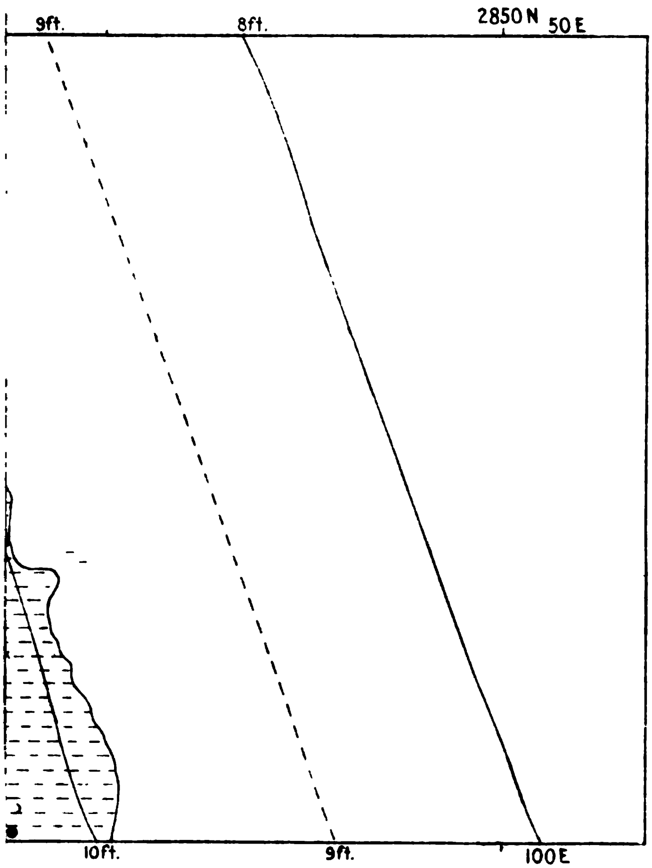
The large majority of the plants of *Limonium* about the whole harbor are found between the 6.75 and 7.75 foot levels. On well-drained peaty soil, such as turfs of *Spartina patens*, *Limonium* may get down to 6.5 feet, while on hard, gravelly beaches, out of reach of fresh water, it may go up to 8 or, in one instance, to 8.25 feet. It is found only in sunny situations.

Plantago decipiens on the upper littoral belt: This narrow-leafed fleshy perennial is found in this belt at three or four points about the head of the harbor, on gravelly or half-drained peaty soils between the 6.25 and 8.25 foot levels (160 south by 1,090 east, 400 to 480 north by 1,040 east, and 20 south by 730 east, etc.) (plate XIII). It is rather surprising that this plant has not been seen on some of the gravelly beaches of the Spit and west side of the harbor, unless it be the abundance of fresh water in the latter case and perhaps the poor drainage of the former, due to humus packed between the pebbles.

Samolus has been seen at but one point in the upper littoral belt (200 north by 1,050 east), where it grows between the 7.5 and 8.25 foot levels associated with *Juncus Gerardi* and *Salicornia*, and near its upper limit bordered by *Teucrium canadense* and *Psedera quinquefolia*.

Scirpus nanus is a diminutive species that occurs in the upper littoral belt somewhat more abundantly than either of the last two species. It usually forms dense turfs, sometimes a meter or more square (122 south by 1,089 east), and grows on fine-grained peaty soils that are often bare, or nearly bare, of other vegetation, except algæ such as *Rhizoclonium* and *Vaucheria* (plates XXI and XXII). The seed plants most often found with this *Scirpus*, when any are present, are *Salicornia europæa*, *Distichlis*, *Atriplex patula*, and occasionally *Spartina glabra*. *Scirpus nanus* is confined to a half dozen locations on the Marsh (*e. g.*, 500 south by 700 east, 25 north by 1,100 east), one area on the east shore near the mill (400 to 480 north), and two areas on the west shore (660 north at 7.5 feet and 850 north at 7 feet). The soil on which this plant grows is always pretty completely saturated with salt water, the fine texture of the soil enabling it to hold the water well from one high tide to the next. At 6 south by 1,050 east, at 7.33 feet, this plant was growing well at the margin of a tide-pool, the surface of which, for the purpose of killing mosquito larvæ, had been kept covered during the summer with crude petroleum. The *Scirpus* we are discussing occurs chiefly in sunny spots, and between 6.5 and 7.5 feet, although it has been found as low as 6.25 and as high as 8 feet.

PLATE XIV,



Spergularia marina is a fleshy annual occurring in this upper littoral belt, which has been found during most summers in a half a dozen locations on the Marsh, in two areas on the eastern shore, and in two or three areas on the west side (plate XIII). It has not been recorded from the Spit. The areas mentioned on the east side are on the well-drained top of the old stone wharf (950 north at 7 to 7.5 feet) where scores of plants were found in 1912, and a stretch of beach between 300 and 470 north, along the whole of which only 40 or 50 plants were found, some of them near fresh-water rivulets, but not where the soil could be really saturated with fresh water. The four areas at which *Spergularia* has been found on the western shore are 1,020 north at 7 to 7.5 feet, 1,210 north at 7.75 feet, 1,400 north at 7 feet, and 2,090 north at 8 feet. Two of these are in the neighborhood of fresh-water streamlets, though not where the soil can be saturated with the water from them. It is possible that these streamlets favor the *Spergularia* only as they allow better drainage of the soil on which it grows by cutting channels through this peat clear down to the underlying gravel. The second and fourth areas cited for the west side are far larger and more densely covered. There are 10 sq. meters dominated by *Spergularia* at 2,090 north. On the Marsh, the highest plant, a single one, was near the 8.75-foot level (298 south by 1,075 east). More commonly it was found between the 6.5 and 8 foot levels. It occurs in dozens near 90 south by 1,080 east, and also by the edge of the tide-stream near 100 south by 1,150 east at 6.5 to 7 feet. Still more numerous plants were found on mud covered chiefly by mats of algæ, and with but a few other scattered seed plants, *e. g.,* 10 plants nearly covered a spot 2 meters across at 20 north by 780 east in 1912. Several square meters of soil beneath a bath-house at 20 south by 740 east were thickly carpeted with *Spergularia* in 1912. The most surprising habitat on which a group grew was an undermined block of marsh turf, 1 meter broad and 2 long, that had fallen from the east bank of the Creek, at 150 south by 790 east. This block had probably fallen off 6 months before our observations began, and the plants on it continued to grow well all summer. On the surface of this turf there grew not only the *Spartina patens,* which had held sway over it when in place on the Marsh, but *Atriplex, Salicornia,* and several other seed plants, among them *Spergularia.* While our observations are not complete enough to establish this conclusion, it is suspected that the bettter drainage, from the exposure of five surfaces of this block, instead of one surface, as when it was *in situ* in the Marsh, made it possible for the plants on it to persist there. At the middle level of this block (4 feet) these plants were exposed only 6 hours per tide instead of for 9.5 hours, which was its exposure when the block was *in situ* on the Marsh at 6.5 feet. On the other hand, the time of submergence was doubled, being increased from 3 hours at 6.5 feet to over 6 hours at 4 feet.

Triglochin maritima has been found in the upper littoral belt only on the Marsh and the adjoining portion of the eastern shore of the harbor south of the mill (plate XIII). It is a small perennial having the habit of *Plantago maritima,* being rather thinly sprinkled—a dozen or two plants—among the *Spartina patens* (160 south by 1,075 east and 0 north by 740 east). In other places it is scattered among *Solidago sempervirens* (350 north by 1,000 east), or on gravelly beaches free of *Spartina glabra* (400 to 450 north by 1,060 east). *Triglochin* grows on rather poorly drained muck-like soils, out of reach of fresh water, between the 6 and 7 foot tide-levels, with the exception of one colony on the Marsh that is growing above the 8-foot level.

The only other seed plants found in this upper littoral belt are the occasional inwanderers from the belt above. These are plants that are really characteristic of the higher belt and only push down below the boundary where the soil conditions are unusual, *e. g.*, where it is either gravelly and well-drained, or where it is constantly saturated with fresh water. The most important of these wanderers from the upper belt is *Solidago sempervirens*, of which mature blooming plants have been seen between 7.5 and 8 feet, and seedlings with leaves 1 dm. long have been seen at 6.5, and a few even at 6 feet. But the vast majority of plants of this species grow above the 8-foot tide-line. *Iris versicolor*, which we have included as an inhabitant of the upper littoral belt, is also a plant more characteristic of higher levels, but, probably because above the 8-foot level about this harbor there is more competition and often dense shade, on the springy shores that would suit *Iris*, the majority of plants of this species are found at or just below the 8-foot tide-line.

B. ALGÆ OF THE UPPER LITTORAL BELT.

We have already seen that the firm beach and the marshy shore between the 6.5 and 8 foot levels are inhabited in common by a considerable number of seed plants. In fact, all but three or four of the species that may become dominant between these levels are found on both types of shore.

Essentially the same thing is true of the algæ of this belt. Out of more than 30 species recorded from this upper littoral shore and the wharves at this level 12 may be regarded as dominants, over larger or smaller areas, between seed plants on the shores, or on stones and logs of the wharves. These plants are: *Anabæna torulosa, Calothrix crustacea, C. fusco violacea, Enteromorpha clathrata, Lyngbya æstuarii, L. semiplena, Microcoleus chthonoplastes, M. tenerrimus, Monostroma latissimum, Rhizoclonium riparium, R. tortuosum, Vaucheria thuretii.* Any one of these 12 species may grow more or less by itself, or, commonly, in admixture with one, two, or more other species forming tangles, felts, or incrustations. These mixtures, where seed plants are for any reason absent or sparse, may form coatings over the surface of mud, sand, pebbles, or living or dead parts of the larger plants. These tangles or felts or crusts are found dominating shore areas of from a few square centimeters to many decimeters, or rarely of several square meters, in extent.

Of the 21 other species of algæ found in this belt, some may form small and infrequent tufts, globules, or coatings, but most are scattered more or less sparsely through the felts and incrustations made up chiefly of one or several of the 12 dominant species mentioned above. Most of these 21 species, like the 12 dominant ones, have been recorded from both beach and Marsh, which indicates their pretty general horizontal distribution about this belt. The distribution of the algæ is in this respect comparable with that of the seed plants mentioned above, and helps to give its character to this belt. These 21 less common species of algæ recorded for the upper littoral belt are the following: *Amphithrix violaceæ* (Kütz), *Anabæna variabilis, Calothrix pulvinata, C. scopulorum, Lamprocystis roseopersicina, Isactis plana, Lyngbya lutea, Nostoc* spp., *Oscillatoria* sp., *Polycystis elabens, Rivularia plicata, Rivularia* sp., *Spirulina tenuissima, Cladophora expansa, Enteromorpha intestinalis, Ilea fulvescens, Ulothrix (implexa?), Ascophyllum nodosum, Fucus vesiculosus, Bostrychia rivularis, Hildenbrandia prototypus.*

From the two lists just given it will be seen that, aside from *Ascophyllum, Fucus,* or *Bostrychia,* in occasional tufts and *Hildenbrandia* incrusting the pebbles of fresh-water streams, the algæ of this belt are Schizophyceæ or Chlorophyceæ.

The felts and mats of algæ found on the upper littoral levels of the Marsh and those of the west shore, though similar in general character, are somewhat different in make-up, and, in the commoner constituent species, from the felts and coats of the sandy shore of the Spit. On the soft and constantly wet mud, on the bases of seed plants growing on the Marsh, and on many wet spots on the west shore, the algæ form in some places loose dark or light green turfs or mats, composed usually of several species. In other places green or gelatinous blackish blots occur which are often made up of a single species, nearly pure. On the sandy or gravelly better-drained beaches of the Spit, though loose mats are not entirely wanting, the algæ present are more often arranged in dense felts over the firm mud or sand and in the furrows between the pebbles. Others may form compact leathery or slightly spongy, dull blackish incrustations over the projecting surfaces of the pebbles of the beach (plate X B). The first type of association, the tangles or felts on sand or mud, are scattered quite generally along the whole south shore of the Spit, between the 6-foot and 7.5 or 8 foot levels, but chiefly between 6.5 and 7 feet. On sunny days, the firmer of these felts on the more sandy mud of the beach dry out and crack into numerous small polygonal sheets, several centimeters across and a millimeter thick. These curl up at the edges and may peel off sufficiently from the substratum to be floated to a new locality at the rise of the tide. Associations of the second type referred to, the dense incrustations on pebbles, or more rarely on shells, simply dry, during low tide, to thin, hard coats, adhering tenaciously to the surfaces of the pebbles. The tangles or mats found about the bases of the seed plants of this shore are looser and more like those found on the Marsh and on the west shore. These dry out to curly or cobweb-like tangles hanging loosely about the stems of their supports.

The distribution of the tangles, turfs, felts, and crusts of algæ on the Spit has been fairly constant during the several years our study has been in progress. Detailed notes made in 1908 and 1910 show essentially the same distribution of the various types of association of the algæ of this belt. It is as follows: Beginning at 1,000 west we find rather sparse loose felts on sandy mud beside the footpath among *Spartina patens,* etc., at 7.5 to 7.75 feet. These felts are made up chiefly of *Lyngbya, Microcoleus,* and *Oscillaria,* but with considerable *Rhizoclonium* and some *Vaucheria.* From here on eastward to 800 west, we find the soil covered with a thin felt from which *Rhizoclonium* and *Vaucheria* have about disappeared, while *Calothrix* is more abundant than farther west, forming a blackish coat on pebbles. From this point eastward to 670 west, the felt is sparse, and chiefly of *Lyngbya, Microcoleus,* and some *Rhizoclonium* near the 6.5-foot level. From 670 west eastward to 560 west there is a considerably denser felt, chiefly of these same Schizophyceæ, on the soil of the areas dominated by *Salicornia* and *Suæda,* and certain intermittent areas of the pebbly beach have black incrustations of *Calothrix,* etc. From 560 west to 430 west thin felts of these same Cyanophyceæ are found only on shaded soil between 6.25 and 7 feet, and crusts occur on the sides of some pebbles in the shade of *Suæda* or *Spartina.* *Rhizoclonium* is found here but infrequently at these

higher levels, and is not wanting from among the *Spartina glabra* at slightly lower levels. Eastward of 430 west to 150 east the algal felts and crusts are wanting over most of the loose, gravelly beach. Only where the soil is bound together by clumps of *Spartina patens* do we find small bits of loose alga felts on the bases and dead leaves of this grass. From 150 east to 580 east, between 6.25 and 7 feet, there is a green or blackish felt or crust over all unoccupied mud, sand, pebbles, or bits of stubble of *Spartina patens* and *Salicornia europæa*. Not merely are the edges of the pebbles incrusted but the tops of those 4 or 5 cm. across are completely covered. The composition of these felts, which are best developed on the Spit, includes the following species: *Calothrix* (2 species), *Lyngbya* (3 species), *Microcoleus* (2 species), *Oscillatoria* (2 species), *Pleurosigma, Enteromorpha, Rhizoclonium* (2 species), *Vaucheria,* and occasionally *Ilea.* Eastward from 580 east to 870 east the coating of algæ over the soil becomes rapidly sparser and, before reaching the latter point, it disappears altogether. Some *Calothrix, Lyngbya,* and *Rhizoclonium* may still occur on the stalks and dead leaves of *Spartina glabra,* and rarely on the *Salicornia* or *Suæda* at higher levels (plate VIII).

The distribution of the felts or tangles of algæ on the east and west shores and on the Marsh is likewise quite constant and similar in different parts of the shore-line, except where affected by fresh water or flood-trash. Only on the stone pier at 950 north by 975 east is there any considerable development of the dense incrustations found so generally on the south shore of the Spit. On the gravelly top of this pier, at 7 to 7.5 feet, the pebbles, especially of the northern half, are incrusted by blackish mixtures of algæ. On the north or shaded side of the little mound of soil about each tuft of *Spartina patens,* velvety layers of *Calothrix* may cover many square centimeters, and in a few instances spread over 1 or 2 dm.

Green or reddish crusts may occur along other parts of both east and west shores, on pebbles over which fresh water is flowing. These are made up of green unicellular algæ, of brownish *Ralfsia ?* or the red *Hildenbrandia.* In the tide-pools of the Marsh lying between the 7 and 8 foot levels, we find a still different type of association of algæ. These algæ are chiefly species of *Lamprocystis, Lyngbya,* and *Oscillatoria,* the two latter of which are woven into very firm felts 3 or 4 mm. thick, when moist, and often 2 or 3 sq. meters in extent. These felts may be partially floated and partially submerged at high water, and either lie on the muddy bottom or be supported by sticks and stubble at low water. These felts are very well developed even in tide-pools that are frequently sprayed with crude petroleum to kill mosquito larvæ. New and quite extensive patches of algal felts, especially of *Vaucheria* and *Lyngbya,* may appear in areas denuded of the normal covering of *Spartina* or *Juncus Gerardi.* They are often formed by masses of flood-trash. The algæ may dominate these areas for a season or two, but are usually driven out by the reinvasion of the region by the grass or rush.

We may now take up, in systematic sequence, the thirty-odd species of algæ growing in this belt, indicating briefly the habit and general distribution of each species, taking up the genera of each class in alphabetical order. The distribution of the more important species is indicated on plates VIII and IX.

A. Looking over Marsh at High Tide, from the Causeway at 900 East, toward 2,000 North × 1,000 East.

B. Looking over Creek and Marsh at Low Tide, from the Causeway, at 850 East, toward 1,000 North × 400 West, showing *Spartina patens* (at right); *Scirpus americanus* (middle foreground), *Distichlis* (left foreground), *Spartina glabra alterniflora* (mid-foreground and across middle distance).

THE SCHIZOPHYCEÆ.

To this class belong two-thirds of all the algæ appearing in this belt, as may be seen from the two lists on page 90.

Amphithrix is found on stones in fresh-water rivulets near the lower limits of the present belt, as at 1,000 north on the east side.

Anabæna torulosa Lagerh. (*Sphærogyza carmichæli* of Farlow 1881) is, as we have seen, more abundant and widespread in the mid-littoral belt. Its blackish-green circular patches, however, are not infrequently found between the 6.5 and 7 foot levels, especially on mud beside fresh-water rivulets, occupied chiefly by *Scirpus americanus* (*e. g.*, 1,240 north by 575 west).

Anabæna variabilis is a second species that has been found among felted threads of *Lyngbya* at the 7-foot level, *e. g.*, at 1,720 north on the west side.

Calothrix crustacea is usually the most important constituent of the denser felts and incrustations of algæ which occur on the south shore of the Spit, especially between 560 and 670 west, and 150 and 580 east. These felts are usually found at one or two points each on the east and west shores, *e. g.*, 950 north by 970 east. The most abundant associates of this *Calothrix* in these felts are *Lyngbya semiplena, Microcoleus chthonoplastes, Rhizoclonium,* and *Vaucheria.* The *Calothrix* is found most frequently between the 6.5 and 7.5 foot levels, and on the compact, rather moist soil of a footpath along the Spit, where it is partially shaded by seed plants. It is not found near the fresh-water rivulets.

Calothrix fusco violacea occurs on the stones of wharves, on the Marsh, and on soil and pebbles on both the east and west sides of the harbor at 6.5 to 7.5 feet (950 north by 975 east; 1,060 north by 450 west). It forms dark greenish patches of several square centimeters in extent.

Calothrix pulvinata is a species that forms honey-comb-like spongy coats of 2 to 3 mm. thickness over sandy soil (950 north by 975 east), or on piles and logs of wharves (2,300 north by 1,300 east; 1,060 north by 450 west). It is found at higher levels than the other species of *Calothrix,* being recorded only from between the 7 and 8 foot levels.

Calothrix scopulorum is a fourth species of this genus, and is less abundant than *C. crustacea.* It occurs as a dense black felt, nearly a millimeter thick, on pebbles or very compact soil.

Lamprocystis roseopersicina (Cohn) occurs in a few warm tide-pools on the Marsh, *e. g.*, at 0 south by 1,005 east at 7.33 feet. It forms a thin, light purplish coating over the soft mud, pebbles, or decaying plants in the bottom of the pool. It was found only in places where it would be constantly covered, or at least on substrata that are constantly saturated with salt or brackish water. In April 1911 very little of the *Lamprocystis* was found, and this was confined to narrow bands about the lateral surfaces of pebbles just above the surface of the mud in which they were partially embedded.

Isactis plana is occasionally found in this belt, forming close felts or incrustations over the mud or pebbles, very similar to the more abundant ones of *Calothrix.*

The genus *Lyngbya* is represented in this zone by *L. æstuarii, L. lutea, L. semiplena,* and three or four other less abundant species, which have not been identified. Of these, *L. æstuarii,* the occurrence of which at lower levels we have noted, is the most important because of its more general distribution and its abundance. About the borders of the Marsh south of the harbor, *L. æstuarii* is

a principal constituent of the felts over the surface of the mud, among the *Spartina patens* plants, up to 7 feet (*e. g.,* 25 north by 800 east). Along the west shore *L. æstuarii* gets up to the 7-foot level among *Spartina glabra* in places where the soil is kept barely damp by seepage of water from the shore (1,800 north by 820 west, etc.). On the Sandspit, *L. æstuarii* is rarely found above the 6.5-foot level (500 east), though, as we have seen, it is present just below this level.

Lyngbya lutea is a chief constituent of rather firm felts occurring on wharves and beaches of the west shore. It is found in patches of a few square centimeters in area, up as high as the 7-foot level. This species is also present sparingly at lower levels down to 3 feet.

Lyngbya semiplena and several other smaller species are frequently found together with *L. æstuarii* and its associates about the borders of the Marsh, and also less frequently on the shore of the Spit. *L. semiplena* is the most abundant and widespread of all the Cyanophyceæ on the Marsh. Though the smaller species have not been identified, their size, color, and other characters were noted carefully enough to enable us to determine that they are also widely distributed along the lower edge of this belt, as well as just below it.

Microcoleus chthonoplastes, and less frequently *M. tenerrimus,* may also enter rather sparsely into the make-up of the felts we have mentioned. The former species is found widely, though locally, distributed about the whole shore of the harbor, chiefly between the 6 and 7 foot levels. The gelatinous matrix of these algæ apparently aids in giving substance to the composite felts or more gelatinous incrustations. But *M. chthonoplastes* also occurs on the bare mud between stalks of *Salicornia* or *Spartina* in nearly pure, irregular, olive-green patches, several centimeters across. In these gelatinous patches a sparse admixture of one or more species of *Lyngbya,* of *Microcoleus tenerrimus,* and of an *Oscillatoria* may sometimes be present, which, however, does not destroy the glistening, slimy appearance of these masses.

Two species of *Nostoc* were noted near the upper limit of this belt, in the neighborhood of fresh-water streams. The smaller species, found at 1,010 north by 1,060 east at 7 to 7.5 feet, had cells 3μ to 3.5μ in diameter. It formed brownish gelatinous lobules over the mud. The second and larger species, found at 560 south by 890 east at 7 to 7.5 feet, had cells 5.5μ and heterocysts 6.5μ in diameter. It forms a smooth, brownish coating over the mud.

Aside from the scattered bits of *Oscillatoria* just mentioned, algæ of this genus are not frequent on the mud or pebbles of the shore at this level. Several species occur between these levels on piles, wrecks, and on the bell of a hydraulic ram at 2,380 north by 1,000 west.

Polycystis elabens is a minute bluish-green alga, the spherical cells of which are aggregated in a gelatinous coat over the mud, among plants of *Spartina patens,* on the Marsh at 7 feet above mean low water. It is quite probable that it occurs elsewhere, since it and its associates are so small as to be readily overlooked.

Rivularia is represented by 2 species on the shores in this belt. *R. plicata* is found on the eastern shore near 400 north at 7.5 to 8 feet, on mud among clumps of *Iris versicolor*. The soil here is saturated with fresh water, either seeping or trickling from springs a few feet further up the beach. No salt could be detected by taste in the sap of root or leaf of plants growing in this soil. Of

course, an alga growing on the surface must be immersed in salt water from 1 to 3 hours each tide, except during a few neap tides of each series of neaps. But in the 9 to 11 hours in which the *Rivularia* is exposed, if it takes up any water from the soil, to which it is closely attached, it must be fresh or nearly fresh water. Another evidently distinct species of *Rivularia* was found occasionally between the 7 and 8 foot levels on sunken logs (1,240 north by 575 west).

Spirulina tenuissima: One of the surprises of the study of the felts on the Spit was the discovery of occasional threads of *Spirulina* scattered among the other algæ. It is evidently able to persist here when protected by the other constituents of the felt, and by the shade of the seed plants, though it does not form gelatinous coats, as it does over the *Zostera* near the low-water level.

It is evident from the above description of the distribution of these Schizophyceæ, as well as from the account given earlier of the growth on the wharves, that the 6.5-foot level is not a dividing-line that marks absolutely the upper or the lower limit of distribution of certain of these blue-green algæ. That is, some forms that are equally characteristic of the mid-littoral belt may be rather abundant just above the 6.5-foot level, *e. g., Anabæna torulosa, Lyngbya æstuarii, Spirulina tenuissima,* and *Microcoleus chthonoplastes.* On the contrary, other species that are characteristic of this upper littoral belt may occur in the next lower belt. For example, *Calothrix crustacea, Lyngbya semiplena,* etc., are usually found above the 6.5-foot level, except where unusual local conditions have prevented the *Spartina glabra* from reaching its normal upper limit. In such places the *Calothrix* pushes down the beach to the upper edge of the *Spartina,* even as low as the 6-foot level.

CHLOROPHYCEÆ.

All of the Chlorophyceæ of this belt, with the possible exception of a species of *Ulothrix,* are forms that are characteristic of the belt below. They manage to push up into the present belt, however, in certain especially favorable localities where the shade, the character of the soil, or the running water of tide-streams or fresh-water rivulets render the bottom constantly wet or damp.

The species of green algæ which have thus far been noted above 6.5 feet are the following:

Cladophora expansa is found somewhat frequently on the west shore of the harbor at 7 feet, as a minor component of the looser mats of *Lyngbya, Rhizoclonium, Microcoleus,* etc. It reaches its higher limit of 7 to 7.3 feet near fresh-water inlets, where it forms thin but nearly pure tangles over the soil, between the plants of *Scirpus robustus* (1,670 north by 750 west). A very striking characteristic of this *Cladophora,* as developed at these high levels on the beach, is the sparse branching. This has already been referred to in speaking of this alga in the mid-littoral belt. In many plants the successive lateral branches may be separated by 15 or 20 cells of a perfectly simple main axis. In April 1911, tufts of *Cladophora* were abundant in the Inlet, but nothing could be seen of these tangles of *Cladophora* along the upper beach. It is probable that some of the filaments of green algæ found in the felts above 6.5 feet on the Spit and Marsh are really threads of *Cladophora,* but their shortness and the entire absence of branches make it impossible to determine whether these are fragments of *Cladophora,* of *Rhizoclonium,* or of *Chætomorpha.*

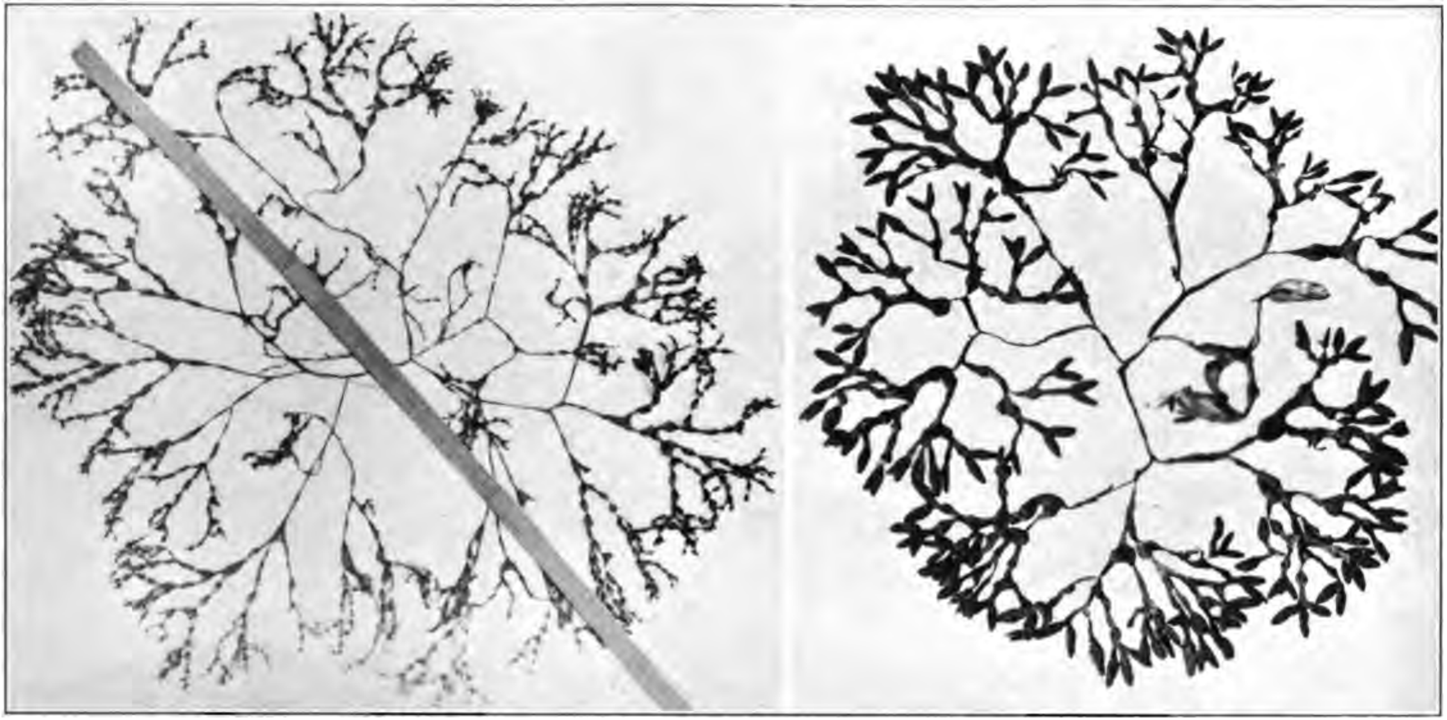
Enteromorpha clathrata is another alga which pushes up beyond the 6.5-foot level. Fragments of this species in good living condition are found matted in the looser felts of blue-greens and *Rhizocloniums* along the west shore, up as far as the 7-foot level. This alga has not been recorded growing at levels above 6.5 feet on the Marsh and Spit, though tangled masses of it are often thrown up by high tides. It seems probable that this species and the associated algæ are able to persist at higher levels on this west shore than elsewhere, because of the greater dampness of the soil, due not only to the abundance of fresh water, but also to the shade from high trees which protect this shore from the drying effects of the sun during low tides occurring in the afternoon.

Enteromorpha intestinalis is a species which is absent from the Spit, but which pushes up into the present belt on the other three sides of the harbor wherever there is a fresh-water rivulet for it to grow in. The upper limit of this alga is pretty constant at 7 feet, the uppermost individuals being relatively small plants of 6 or 8 cm. in height. It is an interesting fact that this species does not push up to a higher level along the shady western shore. This fact seems to confirm the suggestion offered above, that this species, which actually grows in the fresh-water rivulets, nevertheless needs contact with salt water for an hour or two each tide. Its ascent to high levels does not seem to be prevented by any inability to endure long exposure to the air at low tide. Any plants of this species that might locate above the 7-foot level would not be wet by salt water at all for several tides during each series of neap tides, since these minimum tides barely reach the 7-foot level.

Ilea fulvescens, as we have seen, is a characteristic form in certain of the larger fresh-water streams, where its upper limit is in one or two cases as high as 7 feet (1,020 north by 470 west) (plate VIII). It is very interesting to find what is evidently the same species, in active condition, matted with other species on the south shore of the Spit at 6.5 to 7 feet (680 east). It is hard to see what conditions present at this high level on the Spit can make life possible for an alga that is elsewhere accustomed to constant submergence, and, in fact, for most of each tide to submergence in fresh water.

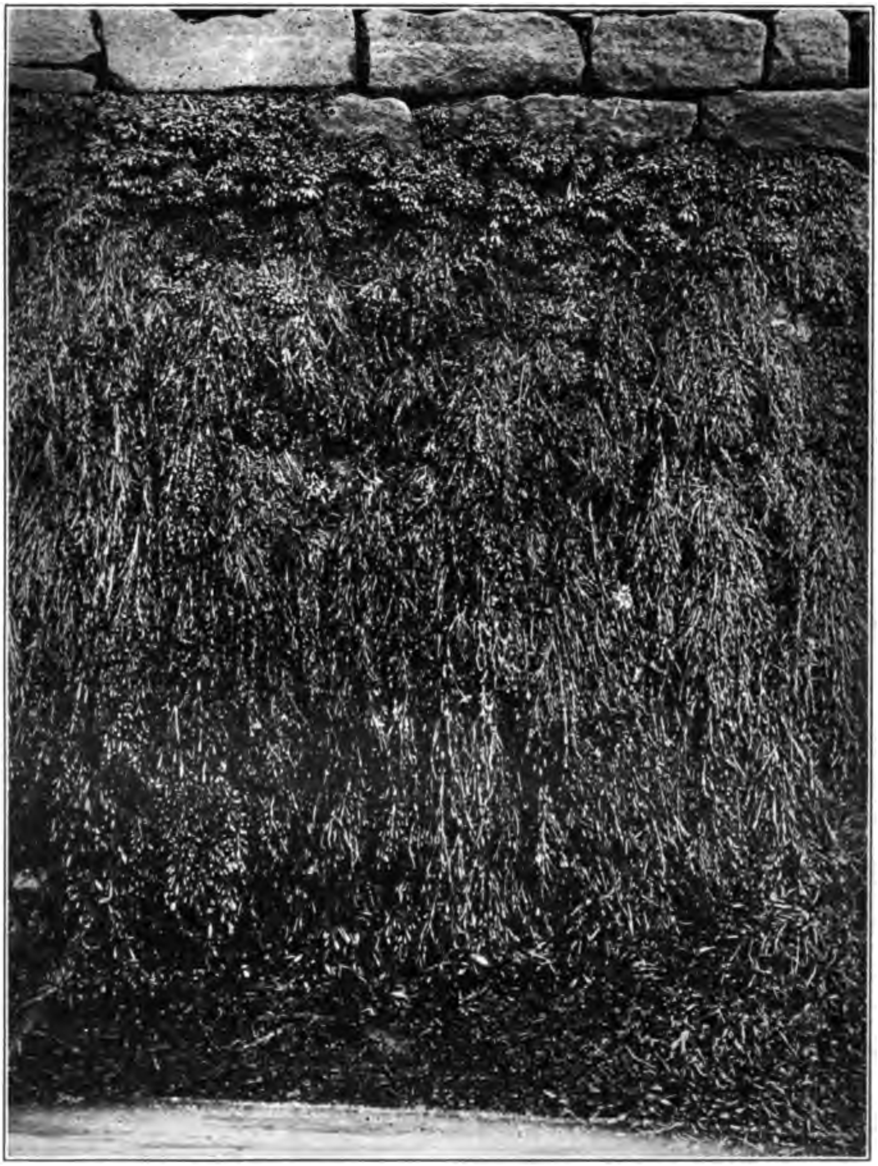
Monostroma latissimum is still another alga associated, as we have seen, with fresh-water inlets. Where these are present it often pushes up to the 7 or 7.5 foot level, as in the Creek south of the harbor (plate VIII) and in several larger rivulets along the west shore. It seems more tolerant of prolonged submergence in fresh water than *Enteromorpha intestinalis.*

The two species of *Rhizoclonium, R. riparium* and *R. tortuosum,* which we have found so generally distributed in the next lower belt, on wharves, and among the *Spartina glabra,* are also the most abundant and widespread green algæ in the present belt. Not only are they widely distributed horizontally about the harbor, but they push far up the beach, often to the 7.5-foot level. In the shade of seed plants on the beach, or among the stones of the wharves, they may occasionally get up to the 8-foot level, or slightly above. In the lower parts of this belt the *Rhizocloniums* are scattered through the firm mats of *Lyngbya, Microcoleus,* etc. At the higher levels they are found in sparse webs, with sometimes a slight admixture of *Cladophora,* clinging about the bases of the seed plants that shade them. The uppermost threads of *Rhizoclonium* seen were associated with a *Rivularia* about the bases of *Iris versicolor* at the 8-foot level (480 north by 1,070 west), or were growing among the *Spartina patens* at



A. *Fucus vesiculosus* var. *spiralis*.

B. An Attenuate Variety of *Fucus vesiculosis*, found on Mud Flats.



Wall of Wharf, on West Side of Harbor, showing Upper Part of Zone of *Fucus* and *Ascophyllum*. growing on Brownstone.

the same level (2,480 north by 800 west). It is worthy of note that these algæ, which push up higher than any others, in fact to levels where they are not immersed in salt water for days at a time, nevertheless always avoid fresh water. Whenever these algæ occur near fresh-water rivulets they are always found just above the level of the water flowing when the tide is out.

One species of *Ulothrix,* probably *U. implexa* Kütz. has been found in this belt at two points on the eastern side, near the 7-foot line, where wet much of the time by fresh water (1,010 north by 1,060 east).

Vaucheria thuretii (or *V. piloboloides* var. *compacta* Collins) is of far less frequent occurrence here than in the belt below, but it does push up into this belt even as far as 7.5 feet at certain places on the Marsh (near 100 south by 1,150 east) and along the shaded western shore. At 1,714 north on this latter shore there is a patch over a square meter in area at 7 to 7.5 feet. This alga, like several others noted above, avoids prolonged immersion in absolutely fresh water, though it is frequently found in the neighborhood of fresh rivulets, on soil kept moist by them.

PHÆOPHYCEÆ.

There are no brown algæ that are truly characteristic of the upper littoral belt. Only two of these from the belt below (*Ascophyllum nodosum* and *Fucus vesiculosus*) ever get up above the 6.5-foot level. Of these, *Ascophyllum* only rarely even reaches to that level on the natural shores, as, *e. g.,* at 1,440 north on the west shore, where it was found attached to stones on the bottom. On the wharves, however, as was noted in speaking of the rockweed association of the belt below, small plants of *Ascophyllum* may develop as high as the 7-foot level in protected places.

Fucus vesiculosus is likewise rare above 6.5 feet, except on the wharves, where, on northern walls, or on the north side of piles, it may occur at the 7-foot level or slightly higher. Two varieties of this species (var. *spiralis* and var. *laterifructus*) sometimes get up from their characteristic habitat in the belt below to the 7-foot level on the shore of the Spit. Nowhere do these rockweeds occur in such numbers as to appreciably affect the character of the vegetation of the shore in this belt. A possible reason for this is a general lack on the natural shores of stones and shells to which the plants might attach themselves. It would seem as if other favoring conditions, such as light, flooding by salt water, and high moisture-content of the surrounding air, must be present here to quite as adequate a degree as on the wharves.

RHODOPHYCEÆ.

As is indicated by our list, only two species of red algæ push up into this upper littoral belt. These are *Bostrychia rivularis* and *Hildenbrandia prototypus,* and each is found at these higher levels only where the conditions are somewhat exceptional.

Bostrychia has been found as high as 7 or 7.25 feet, but when found at this height it is in protected cracks in the stones, piles, or logs of the wharves, or more rarely (950 north by 970 east) on stones in the shade of seed plants, on pebbly shores. This protection from the sun and evaporation is evidently a decided advantage to a plant that is not reached by the high waters of several successive tides in the intervals between the fortnightly spring tides. The

higher individuals of this species are not, like those of the rockweed, dwarfed and sterile, but they bear tetraspores nearly as large as those growing lower down.

Hildenbrandia prototypus, the wide vertical range of which has already been suggested, may push up to the 7-foot level on the shaded rocks of the wharves and on pebbles in the fresh-water streams about the harbor. It may be recalled here that this species does not push up the streams above the limit mentioned, which is the highest level at which they would be surrounded by salt water during more than two-thirds of the high tides of each fortnight.

5. THE SUPRA-LITTORAL BELT, FROM 8 TO 12 FEET.

The borders of the Inner Harbor, between the 8 and 12 foot levels, differ greatly on different sides of it. On the north side there is a rather steep gravelly beach between the 8 and 10 foot levels, then a gentler, more irregular slope culminating in the flattened top of the Spit, at levels between 11 and 12 feet. On the east and west sides the natural portions of the shore in this belt are steep, or very steep, and in most places are well watered by springs or rivulets, so that typical seashore plants are seldom found above 9 or 9.5 feet. The steeper supra-littoral shores on these three sides of the harbor will be designated as the supra-littoral beach, or storm beach.

The supra-littoral levels of the shore on the fourth, or south, side of the harbor form a continuation of the nearly flat Marsh, which we have seen reaches upward from the 1.5-foot level to about the 10-foot level, at the road forming the southern border of our area. This marshy portion of the supra-littoral shore has somewhat brackish soil-water and a different type of vegetation from that on the other sides of the harbor. It will therefore be distinguished as the supra-littoral marsh and will be separately considered.

A. THE SUPRA-LITTORAL BEACH, OR STORM BEACH.

This storm beach, which we are now to discuss, includes the usually steep, natural shores of the east and west sides of the harbor, for 1.5 or 2 feet above mean high water, and the south shore of the Spit from mean high-water level up to 12 feet.

This belt evidently corresponds in part to the zone of "halophilous spermophytic herbs" of Warming (1909, p. 225). But the zone so called by this author includes also other types of plants (*e. g., Salicornia* and *Suæda*), which at Cold Spring Harbor are distinctly characteristic of a lower belt, and occur in the present one only as stragglers near its lower boundary. The present belt also corresponds approximately with the "middle beach" of Cowles (1899, p. 115), but not entirely, since our belt includes much of the beach below the summer storm-line. It is, moreover, quite different as regards the character of its plant covering, in consequence, evidently, of the more protected position of the shores of the small harbor we are discussing.

That this belt or zone is a natural one for the north shore of this harbor, with limits always close to the levels given, will be evident as we proceed. Because of the very general presence of trickling or seeping fresh water, and of the shade of overhanging bushes and trees, the natural shores of the west side and the southeast corner of the harbor, between 8 and 12 feet, differ decidedly in character from that of the north side of the harbor along the Sandspit. In fact,

in many places along the east and west sides, the shore between these levels shows little or no evidence of its proximity to the salt water. On the Spit, however, the environmental conditions within this storm beach belt, and likewise the character of its plant covering, are much simpler and more constant, along the same level from end to end of the beach. We may therefore consider the plant covering here as more typical of the usual shore conditions between these levels, and we will discuss it first.

1. Storm Beach of the Spit (from 8 to 12 Feet).

The character of the soil of the south shore of the Spit up to high-water level has already been briefly described. Above this level and on upward to the top of the Spit, which, from 500 east to 800 west, is on the average 11.5 feet above mean low water, the soil is either of fine gravel or, above 8.5 feet, chiefly of fine sand. There is, however, a small area of firm soil on the top of the Spit at 900 to 1,000 west. Here rubbish from gardens has been dumped, and a heavier soil has been formed, bearing a more varied vegetation. This area, because of its highly artificial and rapidly changing character, will be left out of our further discussion. We must, however, recognize its importance as the source from which many upland plants may have reached the less-disturbed portions of the Spit. Along the western end of the Spit, between 600 and 1,000 west, and between the 8 and 8.5 foot levels, the sand has a considerable admixture of humus. A few patches of similar soil are found between these levels on the eastern half of the Spit near 600 east. On the top of the Spit also, where a denser permanent vegetation is present, *e. g.*, near 600 west and from 0 to 200 east, a considerable amount of more or less decayed plant remains has collected in the sand. Elsewhere the soil is a sand, the dry, superficial layer of which is readily shifted about by wind and water, though the deeper layers are held more firmly by the rhizomes and roots of *Ammophila* and, less frequently, by those of other plants. The slope of the beach, above the 8-foot level, varies from a rise of 1 foot in 40 feet in certain places (*e. g.*, 400 and 600 east, and 900 west), to a steepness of 1-foot rise in 8, 10, or 12 feet along the middle portion of the Spit.

The plant covering of this belt differs from that of the lower belts we have discussed in its sparser character and in its less distinct zonation (plates v, xiii, and xiv). The dominant plant over most of this belt is *Ammophila arenaria*, which spreads from the 8.5 or 9 foot level on the south side, up over the top of the Spit at 11.5 or 12 feet and down not quite so far on the north side. All other species are scattered generally and sparsely over the Spit, or occur in a few local groups. While only 6 or 7 of the 40 species found here have a lower limit of distribution at all closely approaching the 8-foot level, they do range with the *Ammophila* up to the top of the Spit and down the north side. The remaining thirty-odd species are chiefly upland plants, not at all characteristic of sea beaches, and are distributed over the higher parts of the Spit in a manner giving no evidence of clear zonation. The most clearly distinguishable continuous horizontal boundary along the beach, above the *Spartina glabra*, is the sparsely covered, or usually nearly bare, strip of gravelly beach between 7.5 and 8.5 feet. This is the region where the beach is washed by the waves of the Inner Harbor during ordinary high tides of summer. The gravel at this level is more disturbed than at lower levels, the particles being moved about almost daily. In summer it is only when the water has risen to near the high-

water mark that the waves formed in the harbor can force their way through the belt of salt reed-grass to the gravel beach behind it. When the water is at a lower level this grass serves as a complete barrier to the waves. The strip of gravel beach is generally most bare, therefore, where the reed-grass belt is narrowest, and has something of a sprinkling of plants where this *Spartina* belt is wider. (See plates v and xiv.) The plants occupying this gravel strip between 7.5 and 8.5 feet are, as we have seen above, chiefly species from the next lower belt, such as *Spartina patens, Salicornia europæa, Suæda,* and *Atriplex,* though there is in some places a sparse sprinkling just below 8.5 feet of characteristic plants from the belt above, *e. g., Solidago, Cakile, Salsola,* and more rarely of *Ammophila* and *Agropyron.*

The naturalness of the 8-foot line as the boundary between these two belts is evident from such facts as those just pointed out. Of the characteristic species of the upper beach between 6.5 and 8 feet six have been found at, or slightly above, the 8-foot level. But these were in places where conditions were evidently more than usually favorable, and none of the plants ascended higher than 8.25 or 8.5 feet except *Atriplex arenaria,* which is recorded once from 8.75 feet.[1]

The usual upper limit of distribution of the characteristic plants of the upper littoral beach is at the 8-foot level. On the other hand, the normal lower limit for the four most characteristic plants of the Storm Beach is also very near the 8-foot level.[2]

The reason for giving 12 feet as the upper limit of the storm beach is that this is the height of the highest winter storm of which we have definite record. It is also the elevation of the highest part of the Spit and thus of the uppermost soil about the harbor bearing a vegetation that shows the direct influence of the marine environment.

The typical distribution of the six species of plants from the upper beach which wander up into the storm beach, or rather into the gravel strip separating it from the upper littoral beach, is illustrated by the chart of the belt transect of the Spit drawn by Professor Conard (plate xiv). This will be referred to incidentally in giving the distribution of the characteristic plants of the storm beach. It may be noted here in passing that of these plants from the upper beach, only the two grasses, *Spartina patens* and *Distichlis spicata,* are perennial. The other four species (*Atriplex arenaria, A. patula hastata, Salicornia europæa,* and *Suæda maritima*) are annuals, and their exact local distribution in the areas possessing conditions endurable for them varies considerably from year to year.

In view of the fact that the distribution of the plants of the Spit has been mapped in detail (plate v), and that Professor Conard has made a special study of the vegetation of two limited areas (plate xiv and fig. 2), we will only note the more general features of the dissemination of plants growing here.

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[1] These species with their *usual upper limits* and their *extreme upper limits* are as follows: *Atriplex arenaria,* 8 and 8.75 feet; *Distichlis,* 7.5 and 8.5 feet; *Limonium,* 7.5 and 8.25 feet; *Salicornia europæa,* 7.5 to 8.25 feet; *Spartina patens,* 7.75 and 8.25 feet; *Suæda,* 7.75 to 8.5 feet.

[2] The usual lower limits and the extreme lower limits for the species are as follows: *Ammophila,* 8.75 to 8 feet; *Cakile,* 8.5 to 8 feet; *Salsola,* 8.5 to 8.25 feet; *Solidago,* 8.5 to 7.75 feet. (Seedlings were found in one instance at 6.5 feet.)

A. East Side, near 1,800 North, showing *Fucus* and *Ascophyllum* on Pebbles of Bottom, and on Wall from Mean Low Water Upward.

B. Different Stages of Development of *Fucus evanescens*. The Larger Plant shows New Shoots Arising from Stump of a Former Plant, by "Regeneration." × ⅛.

In discussing the distribution of those plants of the storm beach on the Spit which are not found at all below the limits of this belt, we may deal first with the 8 species there found which are confined to sea-beaches or to the similar shores of large inland lakes. Arranged approximately according to their importance, beginning with the most abundant, and indicating the usual upper and lower limits of distribution, these species are the following: *Ammophila arenaria,* 8.5 or 9 to 11.5 feet; *Cakile edentula,* 8.5 to 11.5 feet; *Solidago sempervirens,* 8 to 11.5 feet; *Euphorbia polygonifolia,* 8.5 to 10 feet; *Lathyrus maritimus,* 10 to 11 feet; *Xanthium echinatum,* 9.5 or 10 to 11.5 feet; *Salsola kali,* 8.5 or 9 to 11 feet; *Aster tenuifolius,* 9 to 11 feet.

Ammophila, as has been stated, is the dominant plant over most of the 3 acres of sandy surface of the Spit above 8 or 9 feet (plate VII B). It is a perennial grass with stiff tightly-rolling, partially evergreen leaves. These are 12 or 18 inches high and arise from a buried rhizome that runs extensively (15 to 20 internodes) through the sand. In April 1911, the old leaves of this grass were green for several inches above the soil, and it was the only evergreen form seen on the Spit, unless we except *Salicornia ambigua,* some of the shoots of which were green for 2 or 3 inches above the sand. The stand of *Ammophila* is rather even and not dense, varying from 50 to 200 plants per square meter (plate XIV). The horizontal rhizomes of *Ammophila* run along at a depth of from 5 to 15 cm. below the surface, but the roots penetrate several or many decimeters deeper and thus reach a soil with a pretty constant supply of water, instead of having to endure the very dry conditions often existing at the surface of the sand on which they grow. The lowest surface level reached by *Ammophila* is 8 feet, at which height it is found on the south shore of the Spit, behind the wide border of *Spartina glabra,* at 600 to 700 east (plates V and XIII). The soil here is of very fine sand. The lower limit on the less-protected north shore of the Spit is at 9, 9.5, or 10 feet. Even here it is at a level where its rhizomes are often washed out by the waves during storms.

Cakile edentula is a broad-leafed, fleshy, partially spreading annual about a foot in height. It is scattered over all the more sandy portions of the Storm Beach, between 8.5 and 11.5 feet, and is most abundant near its lower limit. It forms the most important constituent of a distinct green line of scattered vegetation running along the north shore of the Spit just below the *Ammophila, i. e.,* at the 8.5-foot level, *e. g.,* between 400 east and 400 west. This line of plants is made up of annuals, which are evidently from seeds that are caught in the row of flood-trash that settles at this level during high tides. The *Cakile* may, in some seasons, occur somewhat less abundantly, between the 8.5 and 9-foot levels, on portions of the south side of the Spit. Thus, in the summer of 1910, a rather compact group of 40 plants occupied the low spot 2,515 north by 790 to 800 west, at the 8.75-foot level. Plants of this species occurring on the higher levels of the Spit are usually quite scattered, but may, under favorable conditions, be grouped in dozens even there, as, *e. g.,* at 2,800 north by 100 east between 11 and 11.5 feet. It seems evident from the distribution of *Cakile* here noted that this plant will not withstand very prolonged submergence and that it requires a well-drained soil.

Solidago sempervirens, the third in abundance of the plants of the Supralittoral Beach, or Storm Beach of the Spit, is scattered over it in dozens or scores, between the 8 and 11.5 foot levels. It is a lanceolate-leaved, partially

evergreen, slightly fleshy perennial, about 7 to 9 dm. in height. It does not occur in distinct rows or lines, but singly or in small clusters, and its distribution is much more independent of soils and tide-levels than that of *Cakile*. The frequency of the plants may best be illustrated by referring to the map of the area studied by Professor Conard (plate XIV), and also by noting the fact that 75 plants of *Solidago* were found between 400 and 600 west, on the south slope of the Spit. A similar abundance is found at 100 to 200 east, on the top of the Spit, and from 900 to 915 west at 9.5 to 10 feet. From 0 to 200 west this goldenrod is very scarce across the whole width of the Spit, except for one patch of 20 plants on the south slope at 9 feet (see plates V and XIII). *Solidago,* when above the 8-foot level, is a deeply-rooted plant, which draws its water-supply from the constantly damp layer of the sand far below the surface.

Euphorbia polygonifolia, the fourth species of this belt, is a small, spreading, deep-rooted plant that is scattered quite sparsely along the nearly bare sand of the north shore of the Spit, chiefly between 9 and 10 feet, at and below the margin of the *Ammophila.* It occurs still more rarely along certain parts of the south side, at about the same levels. (See plates V and XIII.) This species is so small and the individuals so scattered that it plays no conspicuous part in the make-up of the plant covering of the Spit.

Lathyrus maritimus is another species which is much less abundant here than on the more exposed beaches of the Outer Harbor and Sound. It is a spreading, rather fleshy-leaved, creeping perennial, with buried stems running widely and deeply through the soil. Only a few dozen scattered clumps are present on the Spit, and these are chiefly on the north side of the western half, near the 11-foot level.

Xanthium echinatum, a broad-leafed annual composite, is another plant common on the more exposed shores of Long Island Sound, which occurs somewhat sparingly on the Spit. It is found chiefly on the top and the north side, from 400 east to 400 west, at 10 to 11.5 feet. In a number of places in this area groups of from 2 to 6 plants are scattered quite frequently. Isolated plants are found occasionally on the south shore of the Spit, sometimes down below the 9-foot level. (See plates V and XIII.)

Salsola kali is a small-leafed, fleshy annual, single plants of which are found just above the line of trash from summer tides at the 8.5-foot level on the north shore of the Spit, *e. g.,* from 400 east to 400 west. A few dozen plants altogether may be found at other places on the Spit, as toward the top at 11 feet or along the south shore near the 9-foot level.

All of the last four species are characteristic of the sandy beaches of the outer harbor, where the higher waves form a wider storm-beach, but even here they do not form dense and continuous growths. The chief and perhaps the sole reason for this is the dry and unstable nature of the substratum in which the plants grow. It seems clear that there must be very little real competition with other species in the case of most individuals of these species that do finally succeed in getting rooted, clear of the active waves. In plants so sparsely scattered there is no injury by shading, and it is only in the cases of older plants with extensive root-systems that there can be any appreciable competition for water underground. There can certainly be no accumulation of injurious, excreted waste about the roots of any species in a soil so porous and frequently flushed.

The one remaining species of halyphytic plane found on the storm beach is *Aster tenuifolius*, of which some dozens of plants are present between 600 and 800 west on the south shore of the Spit, at 9 to 11 feet. This plant is a characteristic salt-marsh plant, and occurs on the Spit only in the one place mentioned. The soil here is firmer and has a larger percentage of humus than any soil elsewhere on the Spit. In these respects, and in the somewhat greater moisture content, this soil resembles that of the Marsh south of the harbor, in which *Aster tenuifolius* is found more abundantly.

UPLAND PLANTS ON THE SPIT.

Aside from the 8 species of halophytic herbs or "psammophytes" of the supra-littoral belt, whose distribution has just been described, the 33 remaining seed plants on the Spit are species which also occur on uplands entirely free from the influence of the sea. There are also several lichens, species of *Cladonia*, on the sand, of which only one was found in fruiting condition.

Of these 33 upland plants, 15 are herbaceous dicotyledons, including *Ambrosia artemisiæfolia, Anaphalis margaritacea, Chenopodium album, Euphorbia maculata, Galium claytoni, Gnaphalium (polycephalum?), Lactuca* sp., *Molluga verticillata, Nepeta cataria, Oenothera biennis, Oxalis stricta, Polygonella articulata, Portulacca oleracea, Taraxacum officinale,* and *Verbascum thapsus.*

There are 9 herbaceous monocotyledons, including *Allium vineale, Asparagus officinalis,* and 7 grasses and sedges (*Agropyron repens, Cyperus filiculmis, Eragrostis minor, Panicum* sp., *Poa compressa, P. pratensis, Setaria viridis*). Running over the sand, rather than climbing, are 3 lianes (*Polygonum scandens, Psedera quinquefolia,* and *Rhus toxicodendron*). Finally, there are 6 shrubs or trees, *Ailanthus glandulosa, Gleditsia triacanthos, Quercus* (a seedling found in 1909, absent in 1912), *Rhus glabra, Robinia Pseudo-acacia,* and one plant of *Salix* sp.? 14 feet high. For the general distribution of these see plates V, XIII, and XIV.

Of these 33 seed plants, 23 are perennials, 3 are biennials, and 8 are annuals. The only evergreen species on the beach is *Ammophila*. The shoots of all other species do not push up till late April or early May, and they disappear again in mid-autumn, with the exception perhaps of *Solidago sempervirens,* which is somewhat more persistent. Thus the whole plant, root and shoot, of both perennials and annuals, is probably inactive at the time when the waves of the severe winter storms surround these roots and shoots with salt water. There is, in fact, some question whether the water ever becomes very salt about the deeply buried roots of many of these plants on the higher levels of the Spit, for probably the deeper soil-water is normally never far from fresh. (See Kearney, 1904, p. 424, and Oliver, 1912, p. 98.)

The ability of these plants to invade the upper levels of the Spit, *i. e.,* above the 8-foot level, may thus be in considerable degree due to the coincidence of their period of active growth, and hence of absorption of water, with the season of mild weather and moderate tides. The heavy spring rains must leach out pretty thoroughly any salt left by the high waves of winter storms, and the summer rains are usually sufficient to remove any salt left by the waves of summer storms. Moreover, the soil is usually saturated with rain water before the higher waves of each summer storm are blown on the beach, and hence most of the salt water thrown on the rather steep beach runs off before it can really

penetrate into the soil. Such observations as we have made seem to show that in summer the salinity of the soil water above the 9-foot level, at least on the south side of the Spit, is not very high. These would be in accord, therefore, with the results obtained by Kearney (1904) on the coasts of Virginia, Massachusetts, and California.

Relatively few of the upland plants are able to withstand the conditions encountered near the mean high-water level, *i. e.,* below the 9-foot contour. Those whose lower limit of distribution is below 9 feet are the following: *Agropyron,* 8.25 feet; *Chenopodium,* 8.5 feet; *Galium,* 8.5 feet; *Panicum,* 8.25 feet, and *Poa pratensis,* 8.25 feet. Once we get above the 9-foot level, and thus clear of the influence of summer storms, the conditions become endurable for a much larger number of species. In fact, we find at the 9-foot level, on the shore, or in depressions in the top of the Spit, the only habitats on the Spit for certain species which apparently can not withstand either the greater salinity of the soil-water lower down the beach or the greater dryness higher up. This seems true, *e. g.,* of *Allium, Anaphalis, Gleditsia,* and *Oxalis.* Other species, on the contrary, can endure any conditions found on the Spit except the more saline soil-water found below 9 feet. That is, they range upward from this level to the very top of the Spit, at 11 feet or higher. Such species are *Ambrosia, Asparagus, Eragrostis, Mollugo, Polygonum, Psedera, Rhus toxicodendron,* and *Setaria.* Another series of species have been found only at these higher levels. Thus, *e. g.,* our records show the following plants to have their lower limit between 10 and 11 feet: *Cyperus, Lactuca, Poa compressa, Polygonella,* and *Portulaca.* Finally, another series still of the plants of this belt, which includes most of the woody species, have not been found growing below the 11-foot level. The chief of these are, *Ailanthus, Nepeta, Oenothera, Quercus, Rhus glabra, Robinia, Salix,* and *Taraxacum.*

The further details of distribution of the plants of these levels on the Spit are shown in plate XIV, in which the individual plants of a selected transverse strip of the Spit are indicated by a symbol for each individual, except in the case of a very numerous dominant species. The significance of this chart, and of plate IV, giving the zonation of vegetation on another selected part of the Spit, will be made entirely clear by the full explanation accompanying each of them.

2. The Supra-Littoral Beach, or Storm Beach, of the East and West Sides of the Harbor (from 8 to 10 Feet).

On the east side of the harbor there is, as noted above, no really natural shore north of the mill at 500 north (plate I). There is, however, a border of rather gravelly soil between the 7.5 and 9 foot levels, extending from about 800 north to 1,150 north and including the eastern half of the stone pier. The wall of the wharves here varies from 7.5 to 8.5 feet in height and is often of loosely laid stones, which allows the water to wash away the soil behind the wall, often down to considerably below the top of the latter. This strip of shore has somewhat the character of the same levels south of the mill, except that it has fewer fresh-water streamlets. The vegetation of this soil includes half a dozen species characteristic of the upper littoral beach, already referred to (pp. 74-90, etc.). There are also 3 species here that are found on the storm beach of the Spit.

These are: *Agropyron repens,* of which occasional tufts are found among, or just above, the *Spartina patens; Cakile,* which may be represented by 2 or 3 plants in some summers (*e. g.,* at 1,000 north in 1911); finally, there is *Solidago sempervirens,* which is the only storm-beach plant that is at all abundant here. In 1912 there were only 4 or 5 small clumps of *Solidago* between 800 north and 960 north, but from the latter point to 1,150 north there were 150 clumps between the 8-foot and 9-foot tide-levels. These grew chiefly on the escarpment marking the boundary between the gravel and the moist, grassy field that lies just shoreward of it.

The very wide vertical range of *Scirpus americanus* is well shown on this shore. From the dense patches of this species already mentioned as occurring near the 8-foot level, at 1,000 and 1,040 north (p. 84), strips of thickly scattered culms push upward, along the banks of the two neighboring streamlets, to the 10.5 or 11 foot levels. (See plate XII.)

There are no species present above 8.25 feet level on this part of this shore, aside from *Cakile, Scirpus,* and *Solidago,* to suggest its proximity to the sea.

South of the mill much of this shore, between the 8 and 10 foot levels, is saturated by fresh water, either running over or seeping through the soil. During the earlier years of our work this water came in part from the mill-race just above, but in 1910 the water of the race was diverted, and the amount of water on the upper levels of this shore has thus been somewhat lessened. The effect of this change on the plants of the shore will probably prove an interesting one to observe. The two projecting points of the shore, near 200 north and 300 north, are somewhat drier and the vegetation differs somewhat from that of the rest of this part of the supra-littoral beach, as we shall see.

An examination of the plant covering of the storm-beach southward from the mill to 500 south shows that, aside from upland species like *Rhus toxicodendron, Solidago sempervirens* is the only denizen of the supra-littoral beach of the Spit that grows above the 8-foot level in this southeast corner of the harbor. *Ammophila, Cakile, Euphorbia, Lathyrus,* and *Salsola* have not been recorded here during the seven years of our study. There are, however, three other coastal species, absent from the Spit but found on the supra-littoral marsh, that occur along with *Solidago* between the 8-foot and 9-foot levels of this shore, namely, *Baccharis halimifolia, Hibiscus moscheutos,* and *Iva oraria.*

The *Solidago* mentioned is found generally and rather abundantly distributed from 500 north to 200 south. For example, there were 50 plants of it between 300 and 500 north in 1912, some of them being below the 8-foot level. It is still more abundant near 200 north and near 200 south by 1,200 east and far less abundant in most of the intervening region, where the shore is more nearly saturated with fresh water, and more shaded (see plate XIII).

Of the three marsh species on this part of the storm-beach, *Baccharis* is least frequent, being represented by one small bush near 110 south by 1,220 east at 8.3 feet. Of *Hibiscus moscheutos* there is one clump near 175 north at the 8.2-foot level and half a dozen more along the fresh-water ditch from 150 to 400 south by 1,180 east. *Iva* is rather frequent. For example, one bush at 210 north, 6 at 180 north and a clump of 50 four-year-old plants near 165 south by 1,200 east at the 8.5-foot level. In 1912 there was a group of 30 seedlings, from 2 to 6 dm. high, near 110 to 130 south by 1,150 east.

It is worthy of note that those species of the next lower belt, which on the Spit may wander up to 8 or 8.2 feet, seldom get above 7.5 feet on this part of the eastern shore. Only at one drier spot here (320 north) do we find a few plants of two of these (*Atriplex patula* and *Limonium carolinianum*) growing at 8.2 feet. Not only is this true, but *Spartina glabra* itself is forced down to the 6-foot level on the wetter parts of this shore. The general effect of the abundance of fresh water in the soil is to push the upper limit of the mid-littoral and upper littoral associations downward to 6 inches below their usual levels, on the Spit, on the Marsh, and on the more exposed parts of the western shore.

On the other hand, the abundance of fresh water in the soil of this east side allows certain upland and fresh marsh plants to push down to considerably lower levels than usual. Thus, *e. g.*, we have noted (p. 87) that *Iris versicolor* is scattered along this shore, sometimes as low as 7.5 feet (at 10 north, 350 north, 400 north, etc.). The soil about the roots of these plants is thus probably fresh, though the sturdy leaves and flower stalks are submerged in salt water daily, except during the smallest neap tides. In like manner *Samolus floribundus* pushes down to the 7.5-foot level, where its shoot is also regularly submerged in sea-water, but its roots remain embedded in a soil saturated with fresh water. These cases illustrate an advance of these species into areas below their usual lower limit, similar to that of *Scirpus americanus* on the west side, *e. g.*, at 1,230 north, where this plant follows the fresh-water rivulets down far below its usual lower limit of 6.5 or 6 feet.

A considerable number of other swamp or fresh marsh plants, though not, like *Iris*, found below mean high-water level, do grow just above it, where their roots and parts of their shoots are covered by the higher tides during the growing season. Among such forms the following are of interest: *Aspidium thelypteris* occurs in several clumps at 8.7 to 9 feet (near 400 north). The tall shrubs *Benzoin æstivale* and *Clethra alnifolia* are found on wet, springy banks at 8.5 to 8.8 feet (*e. g.*, 10 to 70 north); *Cicuta maculata* is found occasionally in saturated soil just above the 8-foot level (110 south); *Eupatorium purpureum* and *Lysimachia terrestris* also occur as low as 8 feet near the latter point; *Sagittaria latifolia* forma *obtusa* grows at the 9-foot level in an area where fresh water is present in the soil, though not abundant enough to run off from the surface (near 200 north); finally, *Symplocarpus fœtidus* also pushes down below the 9-foot level (*e. g.*, 110 south).

The highest storm-tides observed during the session of the Laboratory, July 1 to August 15, reached slightly above 10 feet. Night tides rising to 8.5 feet or more occur for several days in succession during spring tides. It will be interesting, while keeping in mind the height of these extreme summer-tides, to note the more important inland plants, besides the few marsh plants just mentioned, that have been seen below the 10-foot level on this wet eastern shore. The following are the more important of these species, with the lowest level at which each has been found: *Alnus incana*, a number near 200 north at 9 feet, on soil rather dry at the surface; also dense clumps, 12 feet high, at 9-foot level, from 50 to 100 south; *Ambrosia artemisiæfolia*, near 350 north at 9 feet; *Asclepias incarnata* near 100 south, at 8.2 feet, in very wet soil; at 350 north in better drained soil at 9 feet; *Convolvulus sepium*, 200 north, at 8.5 feet; *Daucus carota*, 350 north at 9 feet; *Equisetum arvense*, 400 north at 9 feet; *Eupatorium perfoliatum*, 110 to 120 south at 8.2 feet, and 350 north at 9 feet; *Hypericum*

virginicum, 350 north at 9 feet, and rather generally along this part of the shore: *Impatiens biflora*, 350 north and scattering to 110 south at 9 feet; *Juncus canadensis*, 400 north at 8.5 to 9 feet; *Lycopus virginicus*, 340 to 360 north at 9 feet; *Prunus serotina*, 355 north at 9 feet; *Psedera quinquefolia*, 110 to 150 south at 9 feet; *Pyrus malus*, 320 north at 8.5 feet; *Rhus toxicodendron*, 110 south and 200 north at 9 feet and generally along the shore at this and slightly higher levels; *Rhus vernix*, 115 south at 9 feet; *Rosa carolina*, 200 to 400 north at 8.8 and 9.2 feet, and 150 south at 9 feet; *Rubus allegheniensis*, 350 north at 9 feet; *Sambucus canadensis*, 345 north at 8.5 feet, and a clump 5 by 15 feet 480 north at 9.2 feet; *Solidago canadensis*, 350 north at 8.7 feet; *Vernonia* sp., 300 north at 8.5 feet.

THE SUPRA-LITTORAL BEACH ON THE WEST SHORE OF THE HARBOR.

Only a small portion of the west shore above the 8-foot level is now in really natural condition. Starting from 620 south by 680 east and going northward, we find that the upper levels have been much changed. Most of the storm-beach up to the corner of the tide-pond (180 south by 380 east) has been altered by the construction of a walk and a pump-house and by filling in along the lower edge of the garden of the Station for Experimental Evolution. The only characteristic storm-beach plants found along this part of the shore are *Baccharis halimifolia*, *Iva oraria*, and *Solidago sempervirens*. A few beach-plants from the belt below may now and then occur on this part of the shore slightly above the 8-foot level, *e. g.*, *Atriplex patula* and *Scirpus americanus*.

Baccharis is a robust, composite shrub 2 meters high, of which two widely separated plants have been found along this shore between the 8.5 and 9-foot levels (500 south by 650 east, 300 south by 620 east). It is interesting to note that this species is represented by only three other specimens about this harbor (2,200 north by 870 west, 160 south by 1,200 east, 240 south by 1,210 east). It is abundant, however, on the sandy shores of the Outer Harbor.

Iva is an interesting half shrubby composite, sometimes a meter high, which is confined to the Marsh and its eastern and western borders (plates XI and XIII). On the shore we are now considering there is a large clump of these plants near 310 south by 580 east at 8 to 8.3 feet, and a single plant at 500 south by 670 east, while on the north shore of the tide-pool (20 south by 260 to 370 east) some 20 clumps of *Iva* have established themselves on gravelly soil near the 8-foot level.

Solidago sempervirens is scattered in dozens along this whole shore, at and just above the 8-foot level, from the causeway to the tide-pond. It is most abundant on a rather dry, sandy point of the shore near 260 south by 590 east. About the tide-pool at 100 south by 300 east only two storm-beach plants are found. About a dozen *Solidagos* are scattered along the road forming the southern border of the pool. On the gravelly outer edge of the walled wharf from the tide-pool westward and northward to 540 north, at the 8 to 9 foot levels, 75 or 80 *Solidagos* are present; 50 are between 200 north and 400 north. In some seasons these plants are accompanied by a few of *Salsola kali*.

From 540 north to the Spit, on this side the shore, above the 8-foot level, has been less modified than the part south of here, except for the four wharves near, 1,100 north, 1,500 north, 2,100 north, and 2,200 north, respectively. This shore is of a sandy loam, or near the entering rivulets, of black peaty muck.

The shore slopes rather gently downward to the 9.5 or 8.5-foot level, and then by a cliff-like drop of a foot falls to the often gravelly and gently sloping upper littoral beach. In some cases near the streams the beach above and below the 8-foot level forms a nearly continuous slope (plate XIII). The whole of this beach between the *Spartina glabra* and the dense growth of inland species is often only 2 or 3 yards in width and 1.5 feet in vertical range. The consequence is that it forms but a slight variety of habitats for denizens of either the upper littoral or the supra-littoral belt.

The only plants of the storm beach along this shore which show any marked effect of the marine conditions are those growing just at the foot of the miniature escarpment, or on top of it, but near its edge. In other words, the real storm beach here has a vertical range of but 1 or 1.5 feet.

Just back of this edge the rich soil is usually well-watered, and bears a dense covering of stream-bank or marsh species of inland types. Most of the shore is well shaded by shrubs and trees of several species to be mentioned later, and this shade also favors the inland rather than the marine species, since most of the latter are not very tolerant of shade. It is probably chiefly because of this shade that characteristic storm-beach plants are few in both species and individuals on this shore. The three species recorded are *Solidago sempervirens,* a few hundred plants; *Xanthium echinatum,* a few scattered plants on well-drained sandy soil (740 to 800 north); *Iva oraria,* a single plant at 2,525 north.

Solidago sempervirens is scattered pretty generally though not evenly along the beach. There are often a dozen clumps in a few yards, and then for many yards there may be none at all or but one or two small clumps. There are 12 to 15 plants between 640 and 700 north; 15 to 20 plants grouped near 720 north; 25 between 740 and 800 north; 20 near 1,000 north, and about 30 clumps at the south end and 20 at the north end of the Research Laboratory wharf. North of this, up to 1,600 north, the *Solidago* is more scattered. Between 1,600 and 1,700 north there are 30 plants. In the next 400 feet northward there are three or four groups of 5 to 20 plants each. On the wharf at 2,200 north, there are 100 plants growing at the 10-foot level. The majority of the plants on this shore are found between the 8 and 8.7 foot levels, although this *Solidago* may get down to the 7.5-foot level and more rarely to 7 feet. It grows beside the fresh-water rivulets, but not in them, and is confined to sunny areas. It seems evident, from the observations made here and on the Spit, that *Solidago sempervirens* does not ascend to higher levels along the west shore because of the competitors encountered. The latter are more abundant and more varied here than along the Spit, because of the better conditions for their growth. The species with which *Solidago* is most often mingled near its upper limit here is *Convolvulus sepium,* though at other points it may be associated with *Rumex obtusifolius* (1,230 north), and more rarely with *Atriplex, Scirpus americanus,* or *Spartina patens.* Its lower limit of distribution may also be regarded as fixed by competition, as it can grow at lower levels, for flowering plants of it were found in 1912 below 6.5 feet (400 north by 1,060 east). It is probably enabled to reach these lower levels because the moderate amount of fresh water in the soil at many points, though not too much for the *Solidago,* is more than can be endured by the competing halophytes from below.

Of the 30 other seed plants found in this belt on the west shore, all are inland forms except 4—*Atriplex patula, Limonium carolinianum, Scirpus americanus,*

A. Looking Northwestward over Marsh, from 1,150 East on Causeway. The Symbols indicating Vegetation are those given on pp. 153-156.

B. Contact of *Scirpus americanus* and *Spartina patens*, near 400 South × 1,000 East. Boardwalk on extreme left. Photo by P M. Collins, 1909.

A. Looking Northward from 900 East on Causeway, over Marsh, showing *Spartina patens* and *Juncus gerardi* (middle distance), *Spartina glabra* (at left), and *Scirpus americanus* (foreground).

B. South Shore of Spit looking Eastward from 200 East, showing *Spartina glabra*, *S. patens*, *Distichlis*, *Solidago*, and *Suæda*. The Numbered Stakes mark Tide Levels on Beach.

and *Spartina patens.* Each of these, as we have already seen, may wander up from the belt below to a little above the 8-foot level.

The frequency and the lower limit of distribution of the 26 species of inland plants found on the western shore between the 8 and 10 foot levels will now be noted briefly. The level given in each case is that of the surface of the soil surrounding the stem. The wet or damp soil mentioned is that which is constantly saturated or nearly saturated with fresh water. We must keep in mind while noting levels what has been said above of summer tides that reach the 9 and 10 foot levels.

Acer rubrum occurs near the salt water at several places. The lowest tree noted (1,375 north) stood on wet soil at 8.8 feet, the leaves of its lower branches being submerged as the tide rose above 8.5 feet.

Ailanthus glandulosa, a large tree at 1,330 north, at the 9-foot level.

Alnus incana is frequent along the wetter parts, and gets down to 9 feet, as at 1,010 north and 1,270 north.

Benzoin æstivale occurs on damp soil at the 8.7 or 9 foot level at 1,000 north, 1,250 north, etc.

Bidens (probably *frondosa*) sometimes gets down to 8.25 feet. In 1912 there was a group of 50 at 1,020 north, and a smaller group at 1,680 north.

Cichorium intybus is found at 8.5 to 9 feet on dry soils, as at 1,050 to 1,100 north. It is remarkable that this rather hardy species, which grows commonly near by, and can withstand submergence in salt water, has not established itself on the higher levels of the Spit.

Convolvulus sepium is found at several places on moderately drained soil as low as 8.5 or even 8.3 feet, where it is sometimes mingled with such characteristic beach species as *Solidago sempervirens, Atriplex patula,* and even *Scirpus americanus* (near 1,700 north).

Fraxinus americana occurs on moist but fairly well-drained soil at the 8.7 and 9 foot level, as at 1,000 north and 1,750 north.

Impatiens biflora is frequent beside the entering streamlets, where shaded, at 8.5 or 9 feet, *e. g.,* 1,005 north, 1,260 north, and 1,650 north.

Iris versicolor is found on rather wet soil, where not too shady, at 8 and 8.2 feet. It sometimes forms clumps a meter across, as at 810 north, 1,000 north, and 1,350 north.

Juniperus virginiana, which is abundant a few yards back from this shore, may get down on well-drained soil to 9.2 feet, as at 1,760 north.

Melilotus alba is found abundantly on damp soil between 8.5 and 9.5 feet on the wharf at 1,050 to 1,200 north.

Panicum sp. has been noted but once on this shore, but is interesting, since it follows a rivulet down from 8.5 to 7.5 feet near 1,220 north.

Periploca græca: One large vigorous vine of this climber, with several dozen stems from 10 to 20 mm. thick, has become established on soil at 9 to 9.5 feet near 1,800 north.

Plantago lanceolata and *P. major* are present, but less common than on the east side of the Harbor. They both get down to 9 feet or slightly below. *P. lanceolata* is found at 1,900 north and *P. major* at 1,260 north.

Polygonum lapathifolium and *P. sagittatum* are established on very wet soils at 9 feet, occurring in one or two spots, as at 1,262 north.

Prunus avium has established itself all along this shore, especially near 1,000, 1,300, and 1,740 north. On hummocks of better drained soil it may get down to 9.25 or even 9 feet.

Robinia Pseudo-acacia gets down to the same level with *Prunus* (at 1,750 north).

Rosa carolina is scattered in wet soil near the 9-foot level, *e. g.,* 1,270 north and 1,750 north.

Rumex obtusifolias occurs occasionally near the 9-foot level, as at 1,230 north.

Sambucus canadensis is not infrequent near the 9-foot level, but two vigorous specimens 8 feet high are growing at the 8.5-foot level at 1,000 north and 1,375 north.

Solanum dulcamara is about as common here as on the eastern shore, and is always found in saturated soil, *e. g.,* 1,030 north at 8.25 feet, and 1,260 north at 8.25 feet, rooted in the bed of a rivulet.

Tilia americana is growing vigorously near 1,760 north at the 9-foot level.

Vitis labrusca is the last of these non-halophytic plants to be mentioned. A large Concord grape which grows on moist soil near 1,670 north, at the 8.75-foot level, fruits abundantly.

The interesting feature of the occurrence of these various plants at the levels mentioned, on most of the west shore, as on the wet and shady parts of the east shore, is the fact that the soil in which they are rooted is often covered by salt water. It may be thus submerged for 3 or 4 hours daily even during the growing season. It is evident that the abundance of fresh water in the soil not only prevents most of the xerophytic storm-beach species from becoming established on these wetter shores, but this fresh water in the soil prevents the salt water from really penetrating it. This soil, saturated with fresh water, aided probably by the shade, enables the inland forms to hold the soil against the storm-beach species that dominate these same levels on the Spit.

In summary, the vegetation of the east and west shores from the *Spartina glabra* belt upward to the 10-foot level is made up of a few types that withstand very salt water about both root and shoot, but can not endure fresh water in the soil, *e. g., Atriplex, Spergularia,* and *Solidago.* Other forms, such as *Scirpus americanus,* withstand fresh water in the soil and a submergence of their shoots in salt water for 3 or 4 hours each tide, but can not withstand shade nor the competition of the inland species. Finally, there are the upland and fresh swamp species, which will not endure salt water about their roots. These grow in soils saturated with fresh water, at levels where this soil and the bases at least of their shoots may be submerged in salt water for only brief periods (1 to 2 hours per tide), during the growing season.

B. THE SUPRA-LITTORAL BELT OF THE MARSH, OR BRACKISH MARSH (FROM 8 TO 10 FEET).

Since detailed studies and maps have been made of the vegetation of the Marsh (plates XI, XXI, and XXII), we may here be content with pointing out the important contrasts between the plant covering of this level of the Marsh with that of the other shores of the harbor, especially with that of the Spit.

A striking feature of the higher levels of the Marsh, at the south end of the harbor, is the absence of the most characteristic plants of these same levels on the Spit, with the exception of *Solidago sempervirens* and an occasional plant of *Atriplex patula.* Plants such as *Ammophila, Cakile, Euphorbia polygonifolia, Lathyrus maritima,* and *Salsola* are entirely absent from the Marsh. In place of these species, characteristic of the gravelly beach of the Spit, we find on the flat, undrained peat of the Marsh a very different set of plants. Here there are extensive stands of *Juncus Gerardi, Spartina patens,* or *Distichlis,* running up to the 8.5 or 9 foot level, there to be mingled with, or suddenly displaced by,

Eleocharis olivacea, Scirpus americanus, or occasionally by *Scirpus robustus.* Finally, at the practically fresh southeast corner of the Marsh, *S. americanus* is replaced by a dense stand of *Aspidium thelypteris* (plates XI and XXI). The sharpness of the boundary often seen between the stands of different species is the more striking because there is no appreciable change in the level or character of the soil. (See plates XI, XIX, and XXI.) There are, however, marked differences in the depth of the peaty soil overlying the gravel subsoil, and also in the salinity of the soil-water, of these differently covered areas (fig. 3).

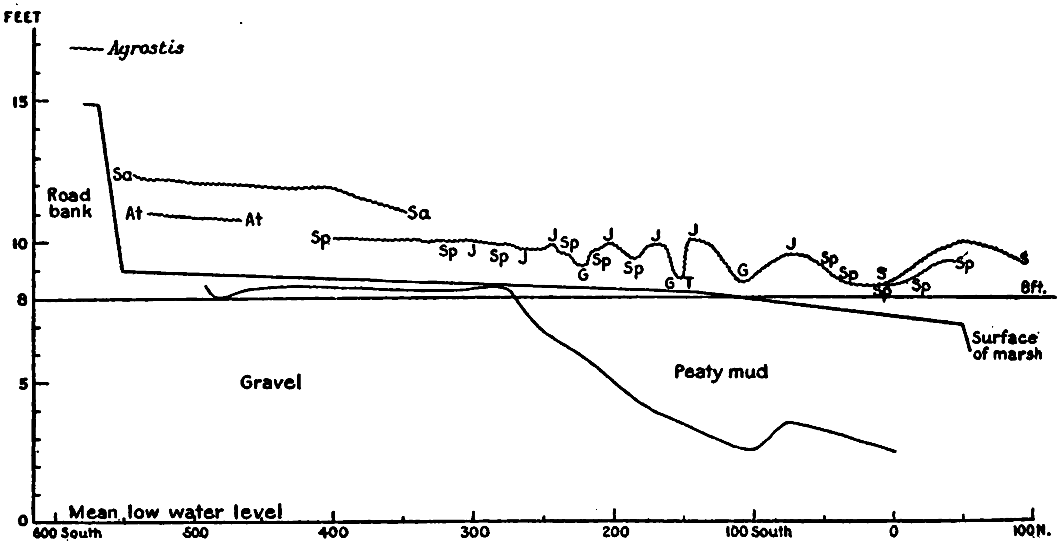
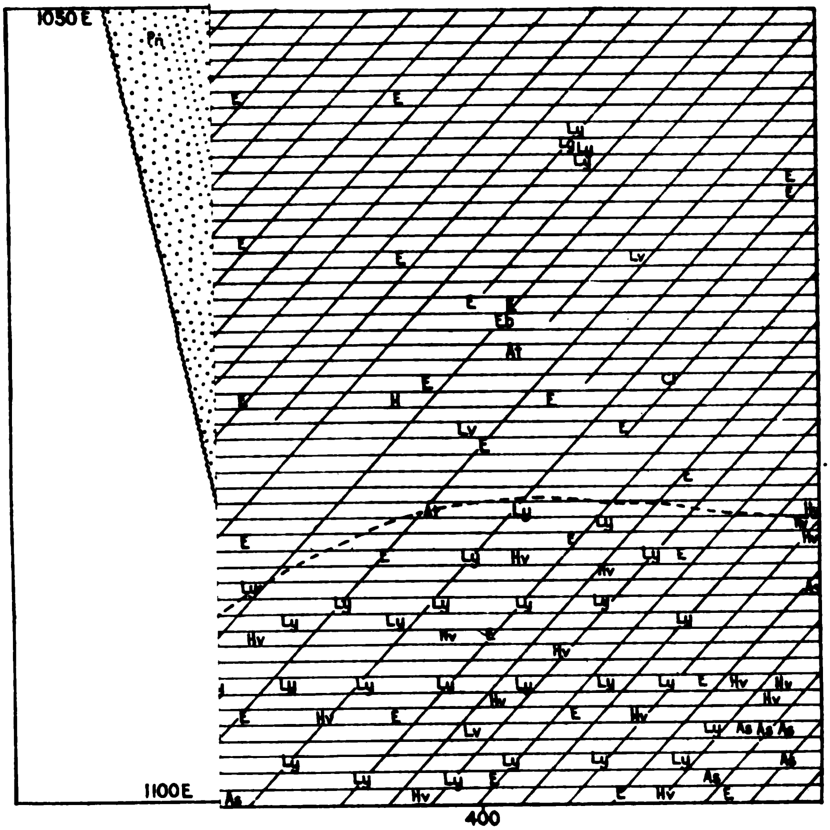


FIG. 3.—Vertical north-to-south section of the vegetation, soil, and subsoil of the Marsh at 1,100 east. Data by H. H. York, H. S. Conard, and P. M. Collins, 1909, 1910. Vertical scale 1 : 80. Horizontal scale 1 : 1,600. ———— indicates height of vegetation above soil. The symbols used are explained on pages 153 to 156.

Among the dominant plants of the higher Marsh are scattered other species, some of which are found on the Spit, but others of which are peculiar to the Marsh or to it and the wetter portions of the east and west shores. Occasionally one of these species may become abundant or even subdominant over a considerable area. Thus *Solidago sempervirens* is scattered thickly along the western bank of the tide-stream from 200 to 400 south at 1,160 east. *Iva oraria,* a bush which occurs at lower levels, also forms considerable patches in this supra-littoral belt, *e. g.,* at 180 south by 1,200 east, and on the west side of the Marsh from 200 south to 500 south. Elsewhere, as about 200 south by 100 east, it is merely sparsely scattered. Still other species may sometimes cover portions of this higher part of the Marsh, of from 1 or 2 up to 30 or 40 sq. meters in area. Thus the rather wet "area 2" of plate VI is dominated by *Triglochin maritima,* which is more characteristic of the belt below. On areas 3 and 27, *Gerardia maritima* is the dominant species (see explanation of plate VI). Areas 25 and 26 are dominated by a thick growth of *Aster subulatus,* while a dense stand of *Pluchea camphorata* is clearly dominant on area 28. *Atriplex patula hastata,* though abundant at several points on the Marsh, is always outnumbered in any considerable area by one or more other species.

The 20 or 25 other species of plants found on the higher parts of the Marsh are never dominant over any appreciable area, but like many of the 15 possible dominants mentioned above, they may be scattered more or less frequently among the species dominating any area. Some of these scattered species may be confined to one or a few small portions of the Marsh, while others, like the *Atriplex* mentioned, may be rather generally, though sparsely, distributed over the Marsh between the 8-foot and 9-foot levels. Certain of these occasional species are, however, rather prominent because of their size, *e. g., Myrica* and *Sambucus;* or because of the brilliancy of their flowers, as is true especially of *Asclepias incarnata* and *Hibiscus moscheutos.*

Further details of the distribution of these plants on the high levels of the Marsh must be sought in the map of Professor Conard. What has been said here is merely to indicate the nature of the marked difference between the plant covering of this wet, partly brackish, sunny marsh and that of the gravelly or sandy, well-drained Spit, or that of the wet, shady, western shore of our harbor.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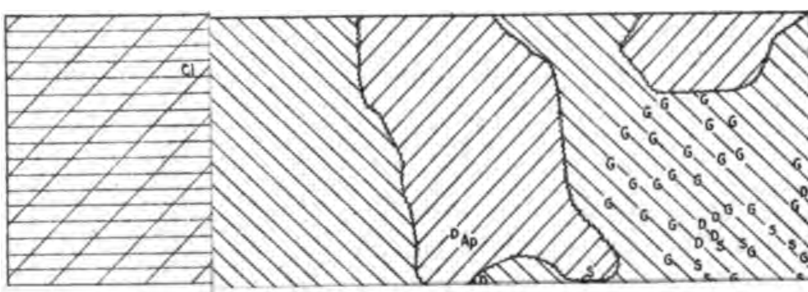

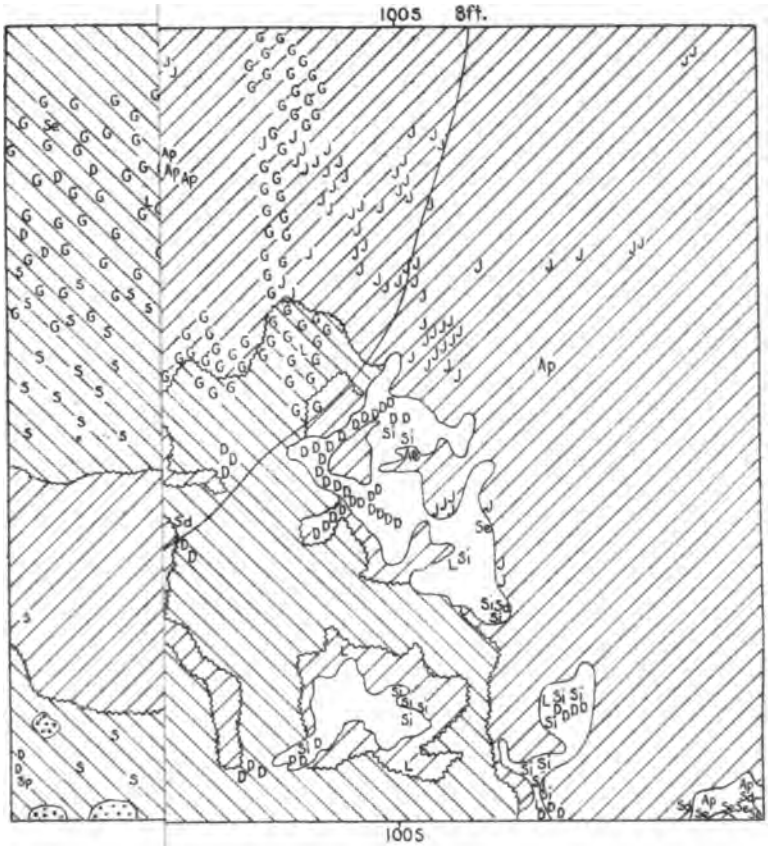
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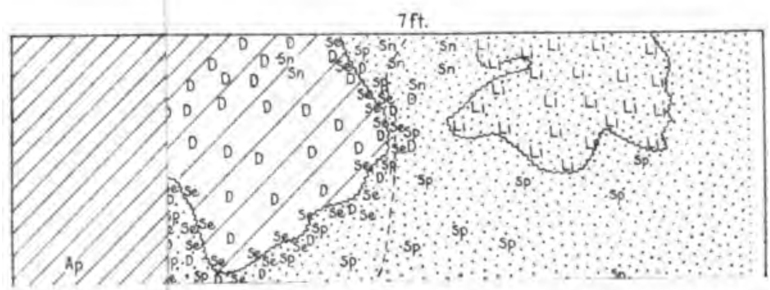
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6. DESCRIPTION AND MAP (PLATES XXI AND XXII) OF BELT TRANSECT OF THE MARSH (FROM 1.5 TO 10 FEET), SHOWING THE DISTRIBUTION OF THE VEGETATION EXISTING IN 1909–1910.

By Henry S. Conard, aided by Paul M. Collins and Charles W. Palmer.

We will give at the start a brief explanation of the construction of the map, plates xxi and xxii. Then, after noting the topography of the area studied, will take up the zonation of its vegetation in detail.

1. EXPLANATION OF PLATES XXI AND XXII.

This map represents a minute study of a portion of the Marsh at the head of the Inner Harbor, by means of a belt transect (Clements, 1905, pp. 178-179). The belt is 50 feet wide and extends from the wagon-road on the south to the open water of the harbor on the north. It lies on the general map between 1,050 east and 1,100 east, and 525 south and 100 north. This belt was chosen because it represents the greatest diversity of vegetation, together with the most distinct zonation. Stakes were set every 50 feet along each side. Then with tape-lines and graduated rods the exact boundaries of the vegetative areas were plotted in strips 5 feet wide. Every plant was located when isolated or not forming a prominent part of a society. For example, every individual plant is given for the following species: *Asclepias incarnata, Atriplex arenaria, Hibiscus moscheutos, Hypericum perforatum, Iva oraria, Myrica gale, Oenothera biennis, Prunus serotina, Rubus allegheniensis, Rumex crispus, Sambucus canadensis, Vaccinium pennsylvanicum.*

Several other species are located where they occur sparsely, or on the margins of their areas, but are put in diagrammatically where plentiful. This serves to show the limits of distribution and the areas of dominance. Such species are: *Aspidium thelypteris, Atriplex patula hastata, Distichlis spicata, Juncus gerardi, Salicornia europæa, Scirpus americanus, Solidago sempervirens, Spartina glabra alterniflora, S. patens, Suæda maritima.*

Carex tenera, Eleocharis olivacea, and *Limonium carolinianum* are marked where sparse, but are not designated on the map where more plentiful. They are mentioned in the description of the various belts.

In every case the mark on the map is much larger in proportion than is the plant itself. This is a mechanical necessity. Hence also many small gregarious species must be diagrammatically shown. Gregarious species which do not become dominant are: *Aster novæ-belgii, A. subulatus, Atriplex patula hastata* (in favorable places), *Distichlis spicata, Gerardia maritima, Impatiens biflora, Juncus gerardi* (when outlying), *Lilæopsis lineata, Lysimachia terrestris* (in favorable places), *Plantago decipiens, Polygonum maritimum, Salicornia europæa* (in places), *Scirpus nanus, Spergularia marina, Triglochin maritima.*

Diagrammatic representation was alone possible for many plants which occur scattered more or less profusely throughout a community. Such are: *Aster*

novæ-belgii, Carex tenera, Eleocharis olivacea, Erechtites hieracifolius, Hypericum virginicum, H. canadense, H. mutilum, Impatiens biflora, Limonium carolinianum (in places), *Lysimachia terrestris, Spartina patens* (in belts of *Juncus, Scirpus,* or *Spartina glabra*).

Some of the above list are not marked on the map at all. Where a series of parallel lines represents a species (*e. g., Spartina patens*), the lines are drawn farther apart where the plant is less plentiful. For symbols not explained on plate XXI see Table F, page 153.

2. DESCRIPTION OF THE STRIP.

A. The Lie of the Land.

The wagon-road on the south of the strip is macadamized, and occupies a causeway built about 6 feet above the level of the Marsh. The bank slopes down to the Marsh as steeply as the earth and gravel of which it is made would lie, that is, about 30°. The foot of the bank is about 9 feet above mean low water. Very high winter tides wash much débris as far as this bank. Thus beds of dead stems of *Spartina glabra* and occasional timbers 6 inches in diameter may be found anywhere over our area.

From the foot of the bank to the 7-foot contour the Marsh forms a smooth plain. The only irregularities are the occasional tide-pools and mud-flats marked on the map. The pools are flat-bottomed depressions of 4 to 6 inches depth. The margins are usually vertical, but sometimes the bottom of a narrow arm of such a pool rises gently to the level of the surrounding sod, forming a mud-flat. Other mud-flats of this region are not connected with any depression. At about the 7-foot contour, in our area, the ground falls off rapidly, or even abruptly. This contour marks the beginning of the dominant and pure growths of *Spartina glabra.*

B. The Plant Covering in Detail.

The vegetation of this strip shows several well-marked zones, or belts, which may be designated along the east side of the strip as follows:

1. Roadside-grass Belt	516 south to 497 south.
2. Fern Belt	497 south to 450 south.
3. *Scirpus americanus* Belt	450 south to 340 south.
4. *Juncus-Spartina* Belt	340 south to 93 south.
5. *Spartina patens* Belt	93 south to 18 north.
6. *Distichlis* Belt	18 north to 28 north.
7. *Spartina glabra* Muhl. var. *alterniflora* (Loisel) Merr.	28 north to 70 north.

1. THE ROADSIDE GRASS BELT OR BELT OF AGRICULTURAL GRASSES.

This area presents a uniform appearance as of a rather sterile and neglected grassy meadow (fig. 1). The grasses are denser and taller on the 2 feet of level ground at the edge of the roadbed. This area is at once seeded and fertilized by washings of manure from the road. The dominant species is *Agrostis alba,* which grows about 20 inches tall.[a] With it occur:

Phleum pratense, *Poa compressa* } subdominant.

Dactylis glomerata, *Agropyron repens*, *Panicum* sp. } sparse.

[a] All measurements of height of vegetation were made after July 15, 1910.

Agropyron attains a height of 30 inches. Dotted here and there occur:

Acalypha virginica.
Ambrosia artemisiifolia.
Aster sp.?
Barbarca vulgaris.
Carex, 2 spp.
Cerastium vulgatum.
Chrysanthemum leucanthemum.
Daucus carota.
Dianthus armeria.
Erigeron canadense.
Hypericum perforatum.
Juncus tenuis.
Lactuca sp.
Melilotus alba.
Oenothera biennis.
Oxalis stricta.
Plantago lanceolata.
Potentilla argentea.
Prunus serotina (2 plants).
Pyrus malus (1 small plant).
Rhus toxicodendron.
Rubus allegheniensis.
Rumex acetosella.
crispus.
Solidago canadensis.
Taraxacum officinale.
Trifolium agrarium.
pratense.
Vaccinium pennsylvanicum.
Various mosses.

So far as these species are indicated on the map, every individual is noted. At the foot of the bank where moisture is plentiful we find also:

Asclepias incarnata (3.3 feet tall).
Eupatorium perfoliatum.
Hibiscus moscheutos (3.4 feet tall).
Impatiens biflora.
Lycopus americanus.
Lysimachia terrestris.
Myrica gale (3.8 feet tall).
Polygonum sagittatum.
Scirpus americanus.

The most peculiar feature of this belt, perhaps, is the group of *Scirpus americanus* which is found 3 feet up the bank, among the grasses. This, together with *Hibiscus* and *Myrica,* owes its presence to the nearness of the salt sea-water. The other plants are such as might be expected on any roadside bank in the Piedmont region of the northeastern United States. The total number of species in Belt I is 45.

2. THE FERN BELT.

Associated with a seepage of fresh water which comes in at the southeast corner of the Marsh, there is a large bed of *Aspidium thelypteris* of dense and luxuriant growth. Overtopping the fern is a sparse but (in our area) universal fringe of *Scirpus americanus.* The ferns are about 2 feet tall, and easily dominate their area (plates XIX A and XIX B). Their border is very sharply defined. They stop off suddenly both south and north without diminution in size or frequency. Outside of this belt only 4 plants of this species occur, namely, at 398 south by 1,072 east, 403 south by 1,081 east, 448 south by 1,098 east, 449 south by 1,089 east. This is doubtless due to the fact that the fern usually spreads by rhizomes, and only rarely by spores. The fern area does not extend quite across the belt. At the middle of the belt there is a narrow strip of marsh between the foot of the road-bank and the ferns. This strip is occupied by a dense and luxuriant growth of *Lysimachia terrestris, Aster novæ-belgii,* and *Impatiens biflora,* the first being dominant and the last least numerous. With these, *Myrica gale* and *Eupatorium perfoliatum* occur as noted on the map. At 492 south and about 1,095 east are two telegraph poles. Between them is a strong bush of *Sambucus canadensis.* This doubtless sprang from a seed dropped by a bird which perched on one of the poles. Seeds dropped in this way are frequent on the marsh. One bird excrement was found containing 11 cherry seeds (probably *Prunus serotina*). Other plants found among the ferns are:

Scirpus americanus (subdominant, averaging 3.2 feet tall, with an occasional maximum of 5.3 feet).
Agropyron repens (beside the telegraph poles).
Asclepias incarnata, *Eupatorium perfoliatum*, *Myrica gale* — as charted.
Erechtites hieracifolius., *Hypericum canadense*, *mutilum*, *virginicum* — abundant.
Aster novæ-belgii, *Impatiens biflora* — frequent.
Panicum sp. (scattered).
Erigeron annuum, *Galium claytoni*, *Juncus canadensis*, *Polygonum sagittatum* — near southeast corner only.
Selaginella apus (3 plants).
A liverwort (*Pallavicinia*).

Atriplex patula hastata occurs frequently, but the plants are slender and etiolated, with narrow, erect leaves. They are hopelessly overshadowed by other plants. Total number of spermatophytic species 19; of pteridophytes 2.

3. THE SCIRPUS AMERICANUS BELT.

Scirpus americanus occurs from the foot of the road-bank to about 345 south, being plentiful throughout this area, and of an average height of about 1 meter. Its inner margin is determined by the road-bank. The outer margin, however, is hardly less distinct. For though the plants become fewer and shorter (2.5 feet), they greatly overtop their companion species. The outlying individuals were easily plotted (plate XIX B). This plant has already been noted as subdominant in the fern area. In the middle of its range it is clearly dominant.[a] Toward its outer borders it is dominant only in appearance. In number of individuals it is greatly exceeded by *Spartina patens*. This grass, beginning at the margin of the ferns in some places, becomes more plentiful by imperceptible gradations, until it becomes dominant, and finally pure (345 south, Belt IV). In the south and east half of Belt III, *Lysimachia terrestris* and *Hypericum virginicum* are frequent at the southeast, becoming sparse toward north and west. *Erechtites hieracifolius* is abundant (about every 4 or 5 feet in August 1909) over the southern two-thirds of the belt. The limits of these plants are shown on the map. *Impatiens biflora* has two outlying representatives at 450 by 1,075 and 445 by 1,050. Single plants occur of *Asclepias incarnata, Aspidium thelypteris* (as already noted), *Carex lurida, Epilobium coloratum, Hibiscus moscheutos, Hypericum canadense, H. mutilum, Myrica gale*. *Trifolium agrarium* and *Rumex crispus* occur at the foot of the road-bank on the south.

Carex tenera and *Eleocharis olivacea* are frequent in the north and northwest portions, the latter species extending as far south as 450 feet and 1,077 east. *Eleocharis* becomes subdominant about 350 south to 360 south and 1,050 east to 1,062 east. Another bed of it occurs at 400 south and 1,075 east. *Carex tenera* is abundant about 350 south to 355 south, where *Scirpus* is becoming decidedly sparse. It grows about 2 feet tall. *Panicum* is sparse throughout this zone. *Lycopus americanus* is represented by 2 or 3 plants near 400 south. *Oscillatoria* was noted on the moist ground at 340 south.

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[a] One square foot near the middle of our third belt was occupied (August 4, 1911) by 48 *Scirpus americanus*, 31 *Carex tenera*, 6 *Aster*, 1 *Erechtites*, 234 *Eleocharis olivacea*, 128 *Spartina patens*. One square foot in the densest patch of *Scirpus americanus* contained 88 stalks of that species, and 32 *Spartina patens*, 1 *Carex*, 2 unidentified grasses, 1 *Acer rubrum* (first year seedling).

A boardwalk runs obliquely across the northern border of the *Scirpus belt*. It is built partly on a low ridge of gravel, hauled in for the purpose, and partly on posts. The gravel forms a strip about 4 inches above the level of the Marsh, and about 5 feet wide. The boards occupy a width of about 2 feet, and the plants for 2 feet on either side of them are kept mowed off with a scythe to a height of about 3 inches. These conditions have greatly affected the adjacent vegetation. *Asclepias incarnata* is especially abundant on the south side of the barrier. *Juncus gerardi* is scattered about in the *Scirpus* belt north of the walk. Between the boards and on the gravel occur:

Agropyron resens.
Ambrosia artemisiifolia.
Anaphalis margaritacea.
Asclepias incarnata.
Aspidium thelypteris.
Aster novæ-belgii.
Atriplex patula hastata.
Bidens frondosa.
Carex tenera.
Dactylis glomerata.
Distichlis spicata.
Erechtites hieracifolius.
Fragaria virginiana.
Lactuca sp.
Lycopus virginicus.
Myrica gale.
Plantago lanceolata.
major.
Prunus serotina.
Rubus allegheniensis.
Rhus toxicodendron.
Rumex acetosella.
crispus seedlings.
Scirpus americanus.
Solidago sempervirens.
Spartina patens.
Taraxacum officinale.
Verbascum thapsus.

Total number of spermatophytes aside from boardwalk area, 20; pteridophytes, 1; additional species along boardwalk, 21; total, 42,

4. JUNCUS-SPARTINA BELT.

The fourth belt is in every way much broken and diversified. It extends from the limits of *Scirpus americanus* to the pure growth of *Spartina patens* at 95 to 150 south. The 8-foot contour cuts its northern border. Many small tide-pools and naked mud-flats break the continuity of the spermatophytic vegetation. With these exceptions, nearly all of the area is covered with *Spartina patens*. In places this is pure, but other large areas are distinctly dominated by *Juncus Gerardi*. So dense is the *Juncus* as to give the impression of a pure growth.[a] Its brown fruits, over-topping *Spartina patens* by 1.5 to 2 dm., give it a characteristic appearance which is noticeable a hundred yards away. But except in some few patches, *Spartina* is always mingled with *Juncus*. On the southern border of our belt, *Juncus* is scattered through the *Scirpus* zone as far as the boardwalk. *Juncus* also occurs scattered in the *Spartina* areas in several places. But the boundaries of the *Juncus* patches are usually very sharp and easily recorded. At 150 south and 1,100 east is a mixture of *Juncus* and *Spartina* which it seemed best to describe as *Juncus* with a mingling of *Spartina* (see plate XXII). .There is a distinct tendency for the tide-pools to be bordered by *Spartina* rather than by *Juncus*. But in several cases one plant borders one side and the other borders the opposite side of the same pool. The average height of *Juncus* is 4.5 to 5 dm.; of *Spartina* 2 to 3.5 dm. or rarely 4.5 dm. In three places (150 south and 1,050 east, 200 to 250 south, 295 to 300

[a] On 5 different plots of 4 square inches each there were counted (August 1911):

Juncus gerardi	17	30	12	5	20
Spartina patens	3	0	0	1	2
Aster subulatus	0	0	0	0	1

This gives an average of 604.8 *Juncus* per square foot. In pure growths, *Spartina patens* averages about 1,400 stalks per square foot. Actual counts gave on 4 square inches, 40 and 43 stalks, and on 16 square inches, 151 stalks.

south, and 1,100 east) *Spartina glabra* occurs scattered among the *Juncus*. It seems to have extended, probably by rhizomes, from denser areas outside the belt. In all such cases it looks starved, and is not over 3 dm. tall. Between 200 and 250 south, *Spartina patens* patches also contain *Spartina glabra*. There is no evidence of antagonism between the two.

In smaller numbers and more restricted areas several interesting maritime plants occur in this belt. *Gerardia maritima* forms distinct beds. Where it occurs, the grass or rush is of very short stature, not over a decimeter, or may be wholly absent. Mud, often containing small pebbles, is visible between the plants. As the grass or rush gradually becomes taller around the *Gerardia* patch, the *Gerardias* become less numerous, taller (up to 2 dm.), and later in flowering. This is evidently due to shading of *Gerardia* by the competitor, reduction of light inducing taller growth, and reduction of temperature causing later germination and slower maturation.

At 150 to 160 south, *Gerardia* is accompanied by the much rarer *Triglochin maritima*. This plant occurs only in the midst of the spots where competition is least. It never, in this belt transect, exceeds 1.5 dm. in height. The individuals are numerous — a hundred or more in each patch. They seem healthy, and flower and fruit freely. At one place about a dozen plants of *Plantago decipiens* are mingled with *Gerardia* and *Triglochin* (160 south and 1,090 east). These were observed in two successive years. They seem healthy, but are of only medium size, about a decimeter tall. In other parts of the Marsh this species attains a height of 1.5 dm. with many leaves and inflorescences to each plant, and *Triglochin* reaches a height of 2 or 2.5 dm.

Spergularia marina was first met at 298 south and 1,075 east—an isolated plant. It is established on the mud-flats about 100 south, in this zone, and on the margins of the next. There were in 1909 about a dozen individuals, 0.6 to 0.8 dm. tall, flowering and fruiting freely. This species and *Plantago decipiens* occur in greater luxuriance outside our belt transect on the inner margins of the *Spartina glabra* zone, where the mud is very sparsely settled by other plants. *Spergularia* was observed in our strip in these places and only in these, both in 1909 and 1910.

Scirpus nanus, miniature but full grown, forms a bed at 122 south and 1,089 east. It is in the edge of a mud-flat, along with *Distichlis, Salicornia europæa*, and *Atriplex patula hastata*. This is much more exposed to sun and wind than the place it occupies in the inner border of the seventh belt.

The scattering plants named above are all essentially gregarious, and not found everywhere. The following are very common members of the vegetation of protected shores, but occur often as isolated individuals:

Salicornia europæa makes its first appearance in the edge of the first large tide-pool (315 south by 1,075 east). In the area from 250 to 300 south many *Salicornias* were dead in 1909, apparently eaten by grasshoppers. Other individuals gave evidence of "damping-off" at the base. The first healthy plants were 282 south and 1,085 east. Between 150 and 100 south many *Salicornias* were large and bushy—excellent specimens of the species. But others were dying at the tips, and some were quite dead. Even the best conditions south of 100 feet are evidently unfavorable to this species.

Atriplex patula hastata was found in a starved condition in the shade of the ferns of the second belt. In the fourth belt it occurs with *Salicornia* in the edge of tide-pools and on mud-flats. The leaves spread out in the normal position and are of normal shape. At 250 to 275 south they were badly eaten by insects in 1909. The first healthy, bushy individuals in our strip, plants 3 dm. high and 2 to 3 dm. across, were in the edges of mud-flats between 100 and 150 south. But just east of our strip fine specimens occur at about 225 south.

Limonium carolinianum was first observed at 300 south and 1,070 east and again at 259 south by 1,068 east. These were small, feeble plants, not flowering. A group of stronger plants occurs at 215 south by 1,075 east. From this point northward the species becomes more frequent and more vigorous. In other places around the harbor it is quite able to hold its own in dense growths of *Spartina patens* and *Distichlis spicata*. It is not hurt by such competition.

Polygonum maritimum seedlings also occur around tide-pools and mud-flats, sometimes in great numbers. Only at 300 south by 1,075 east were they found flowering, and then as slender and weak plants, not over a decimeter tall. In other places on the Marsh a single plant of this species may be 1.5 or 2 dm. tall and as large in diameter.

Distichlis spicata, though occurring along the boardwalk, may be said properly to begin with the tide-pools. It never looks starved, but occurs only in isolated stalks or small groups from 325 to 100 south. In the tide-pools at 100 south and 1,075 east and 110 south by 1,080 east it first shows itself as a real invader, spreading by vigorous straight rhizomes. It is nowhere dominant in this zone.

Eleocharis olivacea does not come farther north than 313 south. *Carex tenera* was not noted outside the *Scirpus* belt, though it was frequent there.

A single seedling of *Iva oraria* was recorded at 300 south and 1,075 east. It was not found in 1911.

One small plant of *Atriplex arenaria* was observed on the edge of a mud-flat at 250 south and 1,079 east.

Seedlings of *Aster subulatus* occur around the mud-flats and beds of *Gerardia*.

Suæda maritima was noted along with *Polygonum maritimum* at 300 south by 1,075 east. This is our only record of this species in this belt.

In a tide-pool in this belt were found seeds of *Prunus* and *Rubus* in bird droppings, and a walnut, a pine cone, and a fruit of *Gleditsia,* doubtless carried by water.

In a pool at 320 south various Cyanophyceæ were noted. A bare spot shaded by grass at 315 south was covered with *Vaucheria*. In a pool at 200 south, and again at 125 south, *Beggiatoa* was found. *Rhizoclonium* was seen partly covered with silt at 225 south, and abundant on the ground among *Spartina patens* at 115 south.

The total number of species in this belt (20) is still considerable, but less than in any of the preceding belts. All of the phanerogams are such as inhabit only saline or brackish soils.

5. SPARTINA PATENS BELT.

A nearly pure growth of *Spartina patens* extends from 100 south to 10+ north, being from the 8-foot contour nearly or quite to the 7-foot. This might be regarded as a large patch from the preceding zone. But its location and

appearance in the whole Marsh mark it off as a distinct area. The grass is very dense and luxuriant, falling over late in the season into irregular hollows and ridges like "licks" on the hair of a cow. Its even, light-green color is especially pleasing to the eye. At 40 north and 1,050 east it reaches a height of 7 dm., 6 dm. at 25 north, and 5.2 dm. at 0 north. Outliers of *Juncus gerardi* extend only as far north as 81 south. Here the *Spartina* is only 3 to 4.5 dm. tall, and at 25 south it drops to 2 or 3 dm. *Atriplex patula hastata, Limonium caroliniamum, Solidago sempervirens,* and *Distichlis spicata* are scattered about irregularly. *Spartina glabra* is scattered plentifully in one place, 0 north by 1,050 to 1,075 east. The southern border of the belt is exactly like the borders of patches in the preceding belt. At 110 south a large bed of *Gerardia* occurs, overlapping the border. On the east side the *Spartina glabra* belt projects into this. The north and west margins of the indentation are formed by the precipitous banks of a tide-creek, and the change of vegetation is correspondingly abrupt. The south margin is a sloping mud-flat. Here *Distichlis spicata* is established, and is vigorously invading. An isolated patch of *Distichlis* east of this may be a relic of an old mud-flat captured by the invading species and then cut off by a later advance of *Spartina patens* across the narrow isthmus. Will *Spartina* finally possess the patch and *Distichlis* withdraw? *Atriplex patula hastata, Salicornia europæa,* and *Spergularia marina* occur in full development around this lobe of *Spartina glabra*. Total numbers of spermatophytes, 10.

In this belt *Beggiatoa,* both white and pink species, were noted in a pool at 40 south, on the contour of 6 feet 6 inches, together with *Anabæna* and mats of *Rhizoclonium.*

About the zero-line the grasses grow shorter and other plants are more numerous among the *Spartina patens*. *Distichlis spicata* in particular appears in rapidly increasing numbers and *Spartina patens* disappears by equal steps, giving way to the *Distichlis* belt.

6. THE DISTICHLIS BELT.

For a short space *Distichlis spicata* is clearly dominant, but it is not sharply demarcated from the preceding belt. On the north, however, it stops with an abrupt but very irregular border at the edge of the tall *Spartina glabra*. The margin is fringed by runners of *Distichlis* advancing northward in the mud, and *Spartina glabra* has numerous outliers of one-half to one-fourth normal height in the borders of *Distichlis*. The narrow strip of soft brown mud (1 to 5 or 6 feet wide) which is not closely occupied by either grass is copiously overgrown with *Salicornia europæa,* together with numerous *Suæda maritima, Atriplex patula hastata,* and an occasional *Atriplex arenaria*. *Scirpus nanus* forms dense mats beneath everything else at several places on the border; at the east edge of the belt this species is quite exposed, forming the sole vegetation over 1 or 2 square feet. Total number of Spermatophyta, 8.

At 25 feet north *Vaucheria thuretii* forms dense tufts on the contour of 6 feet 4 inches, and *Rhizoclonium* was found on a block of wood at the level of 6 feet 6 inches at 25 north.

7. SPARTINA GLABRA BELT.

At 25 to 50 feet north, a tall growth (1 meter high) of *Spartina glabra* becomes the dominant vegetation.[a] Nothing else is apparent. Its inner border has been described above; its outer border is the open water. The ground consists of a soft, brown, oozy mud, whose surface slopes decidedly toward the north. It is cut by many tide-channels from 3 to 18 inches deep.

On close examination we find isolated shoots of *Spartina patens* as far as 10 or 15 feet north of the boundary of this zone. They are represented diagrammatically on the map, actually occurring much closer together than marked. Within 2 or 3 feet of the south margin, *Distichlis spicata* and *Salicornia europæa* are plentiful. *Scirpus nanus* makes a dense growth on the west, just within the border of this zone. The most notable secondary species, however, is the tiny umbellifer *Lilæopsis lineata.* Not over 0.4 dm. in height, it forms a dense sod on the west side of our belt, growing luxuriantly and flowering and fruiting freely. The shade of *Spartina glabra* and two daily baths with salt water seem to furnish the necessary conditions for its existence. It occurs here only, on our strip. Beyond this the seventh belt is a pure growth of *Spartina glabra.* It reaches a height of 9 dm. at 50 north and 13 dm. at 70 north. No other spermatophyte apparently can meet the conditions here. Total number of spermatophytes, 6.

As this belt is the most constantly wet with salt water, it supports the smallest number of species. Are they the most specialized?

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[a] Fifty stalks per square foot (33 on one, 68 on another sample foot).

IV. FACTORS INFLUENCING THE DISTRIBUTION OF LITTORAL PLANTS.

The factors which most directly condition the distribution of littoral plants in this harbor are: the character of the substratum, water-currents, tidal changes in level, salinity of the water, and (probably) the temperature of the water. We will consider these in the order mentioned.

1. SUBSTRATA.

The substrata supporting plants of the shore and harbor bottom may be: (A) living plants or animals; (B) non-living substrata.

A. LIVING SUBSTRATA (PLANTS OR ANIMALS).

The only animal of great importance in serving as an attaching place for plants is the abundant black mussel, *Mytilus edulis.* This has become increasingly abundant in recent years and now nearly covers the bottom over some acres, in the region between 1,600 and 2,000 north by 200 to 1,000 east, and the region between 1,200 and 1,800 north by 200 and 400 west. As we stated in Chapter III, the young mussels become attached to the large sheets of *Ulva* by thousands, so as to make the bottom covered by the *Ulva* and its burden look black. The erectly standing mussels serve to catch the silt and organic débris that is drifting along near the bottom and thus the mussels become partially buried. As the shells of the mussels become larger, firmer, and rougher, the spores of *Ulva* and *Enteromorpha clathrata,* settling upon them, give rise to numberless young sheets or threads of these algæ, which wave back and forth above the upturned edges of the shells of this mollusk. It thus, in turn, becomes a substratum for more plants of the species on which the mussel itself first settled. The *Ulva* and *Enteromorpha* then serve to still further retard the movement of the water near the bottom and thus increase the rate of silting up, until large areas may thus become covered with fine black mud to a depth of 2 feet or more.

Other animal substrata supporting plants are the oyster *Ostrea virginica,* and the various gasteropod shells inhabited by hermit crabs. The oysters of the Inlet, for example, often bear plants of *Agardhiella, Polysiphonia,* or *Ceramium* in addition to the green algæ found on the mussels.

The plants that are most important in serving as substrata for other plants are *Spartina glabra, Zostera,* and *Ulva.*

Most of the species found on *Spartina,* like the *Lyngbyas, Microcoleus, Rhizoclonium,* and *Vaucheria,* are seldom attached by definite holdfasts, but simply tangled about each other over the stalks of this grass in mats. Rarely a few small plants of *Ulva* or *Enteromorpha* are found actually attached by holdfasts.

Zostera really bears a more definitely specialized epiphytic flora than any other plant serving as a substratum. Any of the *Zostera* below mean low water, especially that subjected to the swifter tidal currents, may bear epiphytic tufts

of the diatoms *Melosira* and *Navicula,* of *Enteromorpha clathrata,* and still more frequent tufts of the red algæ *Ceramium rubrum* and *C. strictum.* A single leaf of *Zostera* may often bear two or three dozen tufts of these various algæ, and the leaves are often broken off by the weight of this load, to be finally stranded on the beach. The two *Ceramiums* are practically confined to the *Zostera.* Aside from an occasional plant, on a pebble or shell in the Inlet, these Florideæ find no other resting-place in this mud-bottomed harbor. In addition to these larger forms, *Zostera* may bear thousands of small, sedentary diatoms, like *Cocconeis,* and sometimes many square feet of a stand of *Zostera* may have the leaves fastened together and weighted down by the gelatinous colonies of a *Spirulina.*

Ulva serves not merely for the attachment of *Cocconeis* and other diatoms occurring singly or in very small colonies, but may occasionally bear young plants of *Enteromorpha clathrata* and may also be weighted down by the gelatinous colonies of *Spartina* just mentioned.

Besides the three important species above mentioned that may serve as substrata for epiphytes, many seed plants of the upper littoral belt, such as *Salicornia, Suæda,* and especially *Spartina patens,* may, like *Spartina glabra,* have felts of *Rhizoclonium* and various blue-green algæ tangled about their stems. Finally, any alga in the harbor, if of considerable size, may bear epiphytic diatoms of various species.

B. NON-LIVING SUBSTRATA.

By far the larger number of species found in the Inner Harbor, aside perhaps from the diatoms, grow on a non-living substratum of either purely inorganic or partly organic origin. These non-living substrata may be grouped as follows: (1) soils, including gravel, sand, mud, humus, and peat, among the constituent particles of which the holdfasts, *i. e.,* roots and rhizomes, of the seed plants are embedded; (2) solid substrata, including rock, stones, pebbles, shells, and wood. To the surfaces of these the holdfasts of the various algæ are attached without penetrating appreciably into their substance. Of course, it is evident that felt-forming algæ like *Lyngbya, Rhizoclonium,* etc., may grow on the surface of peat, sand, or gravel. But to these algæ, since they do not penetrate these substrata, the latter are the equivalent of solid substrata. The pebble of the south shore of the Spit is to a *Calothrix* what a stone of the wharf is to a *Fucus* or *Ascophyllum.*

1. Soils as Substrata (Gravel, Sand, Mud, Humus, or Peat).

The soils about the harbor differ in fineness from fine silt or mud up to sand, or even pretty coarse gravel. They differ largely also in the proportion of organic content from nearly pure sand or gravel to humus and peat with a very large proportion of material of organic origin.

There is a very distinct horizontal zonation evident in the general distribution of soils about the natural shores of the Inner Harbor from the bottom up to the 10 or 12-foot level. As has been mentioned in speaking of the distribution of *Zostera,* the portions of the bottom lying below 1 foot are chiefly of a sandy, shelly, or pebbly character. The deep hole near 1,400 north by 600 east, and the deeper parts of the channel leading to the Outer Harbor, have a bottom of

sand and shell fragments which are shifted about by the swift current at each ebb and flow of the tide. The only plants discovered here are those of *Ulva, Polysiphonia, Agardhiella,* etc., which are drifting along and dragging with them the pebbles or shells to which they are attached. To the south and the east of this deep hole there is a considerable area of bottom below the 1-foot level that is covered with a decimeter or more of mud overlying the gravel and which is occupied pretty completely by *Zostera.* (See plate I.) To the west of this depression lies the tide-channel that starts at the Research Laboratory. This channel has a bottom somewhat below —1 foot, with a mud bottom, which also bears more or less scattered *Zostera.*

From the —1 foot level up to the lower margin of the *Spartina* at 1.5 feet practically the whole bottom is of soft brown or black mud. The only exceptions to this are the gravelly east shore of the Inlet, from 1,600 to 2,400 north, and the bed of the Creek, from 100 south to 400 or 500 north. The depth of the mud over the gravelly bottom which underlies the whole Inner Harbor, varies from a decimeter or two up to 1.5 or even 2 meters. The only plants really growing on or in this mud, aside from the diatoms coating certain areas, are *Zostera,* which gets above mean low water near 600 north by 500 east, and *Ruppia,* which ranges from mean low water up to +1 foot. The algæ found growing here on scattered shells, pebbles, or sunken stakes, or on the living mussels, are really rendered thus quite independent of the nature of the bottom. The same thing is true of the floating tangles of *Enteromorpha* and sheets of *Ulva.*

The character of the bottom from +1.5 feet up to about 6.5 feet is pretty constant about the whole harbor, except where changed by entering streams or artificially modified. These levels of the shore consist of a fine-grained, peat-like mud that is more or less firmly bound together by the living and dead rhizomes and roots of *Spartina glabra,* which forms a nearly continuous belt on all natural shores at these levels. The distribution of the *Spartina,* shown in plate I, indicates that of this type of bottom. Only on recently formed gravelly shoals (*e. g.,* near 200 north by 600 east) or at points where smaller entering streams have cut away this peat down to the underlying gravel, or where bathing beaches have been constructed, is this type of bottom wanting about the whole harbor. Along the south shore of the Spit from 800 west to 400 east, it is true, as was noted earlier in the paper, that this peaty bottom does not reach quite down to the 1.5-foot level. The depth of this peat, which usually tapers out to nothing between the 6-foot and 7-foot levels, may be as much as from 3 to 7 dm. in the lower half of the *Spartina* belt. A series of soundings with an iron rod, along a north-and-south line at 10 west, showed a thickness of this layer which at first increased and then decreased in going shoreward from the 2-foot level, in the way indicated in plate V. Essentially the same thickness of peat covers the gravelly bottom on the east and west shores, as is shown by the actual sections of the peat cut by the rivulets entering the harbor over the upper beach (*e. g.,* that at 1,650 north by 800 west).

This layer of peat or peaty mud on which the *Spartina* flourishes is not of the same consistency throughout its thickness. The upper 2 or 3 dm. are firm and fibrous, while the portion below this is far more liquid, so that the upper layer shakes or quakes with the stamp of the foot. The living rhizomes never penetrate far into this less-solid lower layer, which is but little more firm than

the mud covering the bottom of the harbor. The upper, *i. e.*, inshore, edge of the peat belt becomes fairly well drained at low water, due largely to the number of burrows of the fiddler crab *Gelasimus pugilator*. Toward the middle and lower edge of the *Spartina* belt the soil is less firm and is poorly drained, except close to the edge of stream-channels and, in some places, along its own abrupt lower border, at the 1.5-foot level. In these places only do the fiddler-crab burrows, and an occasional muskrat burrow, afford some drainage and an opportunity for aeration.

The only plants usually occurring on this peaty soil besides *Spartina glabra* are the algæ *Rhizoclonium*, *Enteromorpha clathrata*, *Fucus vesiculosus spiralis*, and occasionally *Lyngbyas*, which are matted about the *Spartina* stalks or over the mud. Near the upper margin of this zone of soil, however, occasional inwandering seed plants from the higher levels may be encountered. Of these the most often found are *Solidago sempervirens* and *Suæda*.

On the gravelly soils of the stream-beds there occur *Lilæopsis* at 3 to 5 feet *Triglochin* and *Plantago decipiens* near 6 feet, and the algæ *Enteromorpha intestinalis*, *Monostroma*, *Ilea*, and *Hildenbrandia*.

The soil of the zone above the 6.5-foot level differs much more at different parts of the boundary of the harbor than that below this level, the character at each point depending apparently on the supply of fresh water and on the plant-covering of the same part of the shore just above high-tide level.

On the Spit, *e. g.*, the soils above 8 feet are sandy and dry. In correlation with this we often find between 6.5 and 8 feet a sandy or gravelly soil, with little humus, occupied by felts of algæ or by *Salicornia* and *Suæda*. Trese gravelly and sandy stretches are perhaps due primarily to wave-action, for when the dead *Spartina* stalks have been broken off in the fall, the waves raised by the strong winter winds beat with considerable force against this south shore of the Spit. Alternating with these areas of gravelly soil stretches containing more humus are found, which are occupied chiefly by *Spartina patens* and *Distichlis*.

On the shaded west shore, and on the east shore south of the mill, we find these levels, except for the narrow stream-beds, furnished with a damp, humus-containing soil that is sometimes very peat-like in character. This usually grades off insensibly below into the peaty substratum of the *Spartina glabra*. Above this there is often a sharp cliff-like drop at the boundary between the soil of this belt and the soil of the supra-littoral belt, near the 7.5-foot or 8-foot level. At the bottom of this little escarpment, of a decimeter or two in height, the gravelly or sandy subsoil is often nearly bare of mud. The vegetation of this soil of the upper littoral belt on the east and west shores consists in the better-drained areas, chiefly of *Spartina patens*, and where fresh water is present chiefly of *Scirpus americanus*. In with these are scattered *Scirpus robustus* (near fresh water), *Solidago sempervirens*, and, on more sandy areas, *Spergularia* (plates XII and XIII). Along the rivulets and streams plants of the supra-littoral belt may push down below the 8-foot level.

Along the southern boundary of the harbor, at the north edge of the Marsh, the most marked change in the character of the soil in passing upward from the 6.5-foot level is in the greater firmness and probably larger percentage of organic content of the soil, as it rises abruptly from the 6-foot to the 7-foot level and then slopes up very gradually to the 8-foot or 9-foot level. The upper layer of

soil on this gently sloping portion consists of 2 or 3 dm. of tough, black, fibrous peat, bound together by the dead and living rhizomes and roots of the *Spartina patens*, of *Distichlis*, and of *Scirpus americanus*, by which this part of the Marsh is chiefly covered. A study of the subsoil of this Marsh, by the aid of the section cut out by the Creek, as well as by several series of soundings made with an iron sounding-rod, shows that the firm superficial layer of the peat is underlaid by one of soft, black, peaty mud, of a thickness varying from 1 to 10 or 15 dm. Beneath this is a layer of firm sand or gravel, with a very uneven upper surface, perhaps due to the covering up with the soft muck, of a delta cut by many channels. (See fig. 3, p. 111, which gives a north-and-south section at 1,100 east, as reconstructed from soundings by Professor York and Mr. Paul Collins.) The muck below the surface here is, in consistency, much like that at the bottom of the harbor, and that underlying the firm surface peat of the *Spartina* border about the barbor.

The soil of levels above high-water mark differs very greatly on different sides of the harbor. On the Spit, *e. g.*, there are large areas where the surface layers, at least, are of nearly pure sand, only partially fixed by the tufts of *Ammophila* and occasional clumps of *Solidago sempervirens*. In depressions near the top of the Spit, however, *e. g.*, near 500 east and 800 west, there are patches of firmer soil, rich in humus, and supporting a considerable variety of plants. In fact, wherever a tree or a group of bushes becomes established on the Spit humus accumulates and the soil is held together, so that such areas may be left standing considerably above the rest of the surface, which is lowered by the removal or sand by winds and waves. This is true, *e. g.*, of the area about the *Robinia* near 600 west, of that about the group of *Ailanthus* near 100 east, and of that about the group of *Rhus* at 540 east.

The soil above the 8-foot level on the east and west shores of the harbor, aside from the gravelly artificial surfaces of the wharves, is not much affected by the proximity of the sea. In many places it is springy, wet, and shaded, and most of the plants on it are species found in inland wooded swamps, though *Scirpus americanus* does push up the streams to 9 or 10 feet. In drier, sunny places, beach-plants, such as *Solidago* and *Atriplex patula hastata*, may crowd up among the upland forms to as high as the 8.5 or 9 foot level.

On the Marsh, as we have seen in Section III, the character of the soil and the vegetation changes rather gradually in going southward from the middle of the Marsh at 8 feet to the foot of the causeway embankment at 9.5 feet. These changes in soil and in plant-covering are indicated more precisely in the detailed maps of the Marsh (plates XI, XXI, and XXII). The relation of the vegetation to the substratum is too complex and the causes of its detailed distribution too incompletely understood to make it worth while to take it up in any detail again here, after what has been said earlier in this paper.

In general summary of the relation of the distribution of plants to soils in the harbor, it must be considered as evident: (1) That the sparsity of attached algæ on the bottom of the harbor must be due chiefly to the lack of larger particles in the soft mud to which plants like the rockweeds and red algæ can become attached. Similar tidal basins in the neighborhood, having stony bottoms, show a much more varied algal flora (*e. g.*, Center Island and Lloyd's Point). (2) The peaty mud, commonly found between the 1.5 and 6.5 foot levels, is dominated by *Spratina glabra*, with only a subordinate ground-covering

of green and blue-green algæ. Since, however, this *Spartina* grows luxuriantly in this neighborhood in nearly pure sand, it seems more probable that the *Spartina* determines the character of the soil rather than that the latter conditions the occurrence of the grass at these levels in our harbor, that is, the thick stand of salt reed-grass, between the tidal limits endured by it, favors the deposit of organic as well as inorganic sediment on the surface and also adds considerable organic material by the decay of its own roots and rhizomes within the soil. (3) In the case of the higher levels of the Marsh there seems to be a definite dependence of the character of the plant-covering on the salinity of the soil-water and on the depth of the peat-like layer of top soil. (See fig. 3.) While *Spartina patens* may grow from the 7.5-foot to the 8-foot level, in peat with soil-water of a salinity or specific gravity of 1.017+ at this same level, and in soil of otherwise the same character, except that the soil-water has a slightly lower specific gravity, the plant-covering consists primarily of *Distichlis*. If near the higher level mentioned the salinity of the soil-water gets below 1.006, these two grasses are often replaced by *Scirpus americanus*. (4) The soil differences of most importance in their effect on plant distribution in the two belts between the 6.5-foot and the 12-foot levels on the north, east, and west sides of the Harbor are those in salinity of soil-water, and, especially on the Spit, differences in the amount of humus in the soil.

2. Solid Substrata (Stones, Pebbles, Shells, Piles, and Logs).

The most important of the solid substrata in our harbor are the pebbles of the natural bottom of the Inlet and the stone walls and wooden piles and docklogs of the wharves. The scattered stakes and the shells and occasional stones of the bottom are far less important as plant substrata, the one exception to this latter statement being the shells of living mussels mentioned earlier, with their hundreds or thousands of young plants of *Ulva* and *Cladophora*.

The pebbles of the Inlet consist of well-rounded bits of quartz, granite, gneiss, sandstone, or conglomerate, of all sizes up to 1 or 2 dm. in diameter (plate XVIII). No adequate evidence was obtained of a marked preference of any of the algæ for one material among these pebbles rather than another. The Chlorophyceæ, *Enteromorpha clathrata* and *Ulva,* and red algæ, such as *Agardhiella, Chondrus, Gracilaria, Hildenbrandia,* and *Polysiphonia,* are found more commonly on the smaller, smooth, quartz pebbles, which make up the larger portion of the possible attaching surface on the bottom of the Inlet. The Phæophyceæ, *Ascophyllum* and *Fucus,* on the contrary, are usually found on the larger, rough-surfaced bits of granite or sandstone. It is probable that with the growth of the plants of the rockweeds that happen to start on smaller pebbles the supports are ultimately dragged away by these plants and thus either washed upon the beach or buried in the mud of the bottom of the harbor. This may account for the few quartz pebbles found bearing *Fucus* or *Ascophyllum*. *Ulva* starting on these smaller pebbles may likewise grow and finally drag off the latter. In other cases if the pebble is firmly fixed among its fellows or is too large to be dragged away by the plant, the growing sheet of *Ulva* may be torn loose and float or drift about over the bottom. In fact, the incrusting algæ, such as *Calothrix, Ralfsia,* and *Hildenbrandia,* which grow on the large stones as well as the small, the rough as well as the smooth ones, are the only species which may not finally drag off their supports if the latter happen to be small.

The stone of the wharves about the harbor is chiefly a brown sandstone. There are, however, numbers of large blocks of granite and gneiss scattered among the brownstones of the wharf on the east side, from 1,000 north to 1,600 north. Certain yellowish blocks of this granite and gneiss are constantly bare of *Ascophyllum* and *Fucus,* though all the surrounding stones of otherwise similar character and the brownstone blocks are densely covered by these algæ (plate III). As no differences could be discovered in the chemical or physical characters of the barren and the alga-covered rocks (see p. 70), we have no explanation to suggest for the striking difference in their alga population. In speaking of the gravelly soils above the 6.5-foot level, we have mentioned that *Calothrix, Lyngbya,* or *Microcoleus* are attached to the surfaces of the pebbles of the upper littoral beach, forming "Phycochromaceta" of Warming (1909, p. 175). These simple forms are attached to the surfaces of these fine pebbles and sand grains just as the larger algæ of lower levels grow on the larger pebbles of the Inlet, or of the channels of fresh-water rivulets along the shore (plate X).

The wooden channel-stakes of the middle of the harbor form, as was noted just above, a restricted but often densely populated substratum for numerous algæ. Thus a single stake may bear, attached to its bark, or, in older stakes, to the bared wood, groups of tufts of *Melosira, Navicula, Ulva, Enteromorpha clathrata, Ralfsia, Dasya, Grinnellia,* and *Porphyra,* besides felts or tangles of *Rhizoclonium* mingled with various blue-green algæ. On the larger piles and wharf-logs and on bits of heavy wreckage along the shore, the algal population may be much richer in both individuals and species. Thus, *e. g.,* the vertical chestnut piles of the wharf of the Research Laboratory may bear a dense drapery of rockweeds, any gaps in which are largely occupied by felts of *Lyngbyas* and *Rhizocloniums,* by warty incrustations of *Ralfsia,* by an occasional *Porphyra,* or by dense colonies of *Bostrychia.* In the winter *Ulothrix flacca* becomes prominent on these same piles. Near high-water level occur bands of felted *Lyngbyas* and tufts of *Calothrix.* All of these algæ, except the finer-felted ones, are attached to the firmer parts of the wood, and careful study of sections of the holdfasts of *Ascophyllum* and *Fucus,* of *Bostrychia* and *Porphyra,* show that these do not really penetrate into the tissue of the wood, but simply spread over the surface and into the furrows between the harder strands of the wood. The wooden wharf-logs are generally too near high-water level to bear much rockweed, but they often have an abundant felt or tangle of *Rhizoclonium* even at the 8-foot level when on the north side or where the log is kept moist. At the 8-foot level on logs and stones of the Research Wharf grew the only species of lichen found near high-water mark. This lichen, *Lecanora subfusca,* occurs also at this same level on stakes on the Marsh.

2. THE INFLUENCE OF WATER-CURRENTS.

Under this head are included the effects of water-movement in streams, tidal currents, and waves. Such water-currents may affect the distribution of plants directly, as by wafting about the plankton of the surface and the drifting plants of the bottom, or by the dispersal of the spores or seeds when shed. They may also cause injury or even the total destruction of plants on shores or wharves by carrying ice against them or dropping flood-trash upon them. On the other hand, these currents may affect plants secondarily, by determining either the character of the substratum, the different degrees of aeration of the water over different areas, and finally by a favorable or unfavorable effect on competitors.

The plankton organisms, such as the Diatomaceæ and Peridineæ, are often drifted together in certain corners of the harbor by tidal currents and winds till they color the water deeply, while other parts of the harbor are comparatively free from these plants. The distribution of many Chlorophyceæ and Florideæ that are free or attached to small supports is changing constantly and they drift with the tide. The ultimate results of this drifting is often the stranding of these plants so high up on the bottom or shore of the harbor that they are killed by exposure. We have mentioned in detail in Section III (pp. 18, 21), the repeated redistribution of plants or fragments of *Ulva* and *Enteromorpha clathrata*, and the same process must be very active in the case of *Fucus vesiculosus spiralis* in late winter and early spring, when the wearing off of the dead stalks of *Spartina* by ice and waves has left the *Fucus* free.

It is evident that spores or seeds discharged into moving water may be carried to very considerable distances by it. The seeds or spores of plants, *e. g.*, those living in the tidal channels, must thus be distributed widely over most or all of the habitats suitable for them, as well as over many others. We suggested above (p. 32) that certain Florideæ, of sporadic occurrence in the Inner Harbor, probably arise from spores which are brought in by the tide from neighboring areas in the Outer Harbor, where they are present year after year. A very interesting question that arises here, which can be answered by experiment only, is whether these spores can become attached to surfaces of stone, shell, or wood while the tidal currents are still running, or whether it is only for a short time at slack-water that an effective holdfast can be developed. The cases of algæ like *Ilea* and *Monostroma*, in streams near high-water level, are of especial interest in this connection, since the only period of slack-water in these habitats is that at high water, and then the pebbles on which the spores are to start are surrounded by salt water. The fresh water of the streams at this time, as was shown by Miss Streeter, runs out on the surface of the harbor, leaving salt water next the bottom.[a] It may prove true that the spores of these plants, which are to live most of the time in fresh water, *do*, and perhaps *can*, germinate *only* in salt water. If this is the case it would offer an interesting explanation of the fact that these algæ do not spread up the streams beyond the high-water mark.

In winter, when ice is abundant in the harbor, the plants of the shore, and especially the algæ on the piles and walls of the wharves, are subjected to pretty serious grinding by the cakes of ice and may even be frozen into the ice during very cold weather and then torn off. Tufts of *Spartina glabra*, a meter square, were found in July 1910, many yards away from the nearest *Spartina*. In 1910, *e. g.*, the small tuft at 2,200 north by 750 west was a newcomer. The only plausible explanation we can offer of the appearance of this tuft in an area which in 1909 was totally bare of *Spartina* is that ice froze about the stalks of the plant at high tide, in early winter, and that later, with a higher tide, the clump of the grass, with the peat-mass on which it grew, was lifted bodily and floated by the ice to its present position. In this case the grass has persisted for two (or three) seasons. In other cases, where the turf is dropped in the middle of the harbor, *i. e.*, in deeper water, it does not flourish, probably because of too

[a] Our tests of the Creek at high water of an 8-foot tide showed the presence, just above the bottom, of a stratum of water about 1 foot thick with a density of 1.020 which extended upstream to 600 south. A layer about 2 feet in thickness next above this had a density varying from 1.020 to 1.014. The water at the surface upstream from 450 south is entirely fresh, while from this point northward it increases in salinity to a density of 1.010 at 50 north.

great a proportionate submergence. The algæ on the mud among the *Spartina*, such as *Fucus vesiculosus spiralis* (plate XVI), *Rhizoclonium*, etc., apparently suffer also from the winter waves, aided by the ice. At least they are relatively scarce in the early spring.

On the banks of tide channels, *e. g.*, on the west side of the Inlet, or on the concave banks of the Creek (near 100 south) the turfs of grasses are often undermined by the swift current and many pieces fall into the water to be carried away. Large numbers of plants and very considerable areas of soil are thus destroyed.

Another way in which tidal currents and waves may injure plants is by covering them with tide-trash so deeply as to smother them out. Instances in which *Spartina glabra*, *S. patens*, *Salicornia*, and other species are thus destroyed over areas of several square meters are mentioned in Section III.

Of the secondary effects of water-currents on submerged plants, the most important is probably the effect of this movement on the concentration, in the water about the plant, of solutions of useful and injurious gases or solids, and on the rate of interchange between the plant and the immediately surrounding water. It is a well-known fact that the hard bottoms of swift-flowing tide-creeks, or bottoms just below low-tide mark on wave-beaten shores, have an unusually luxuriant algal flora. While this is partly due to the stony bottom found under swiftly moving water, yet it is evidently attributable partly to the effect of the agitation of the water on the plants themselves. It is probable that all of the effects above mentioned are of importance. But no one, so far as we know, has yet proved experimentally whether the movement of the water is more important in simply increasing the rate of interchange of material between the plant and the surrounding water, or in bringing to the plant solutions of substances needed by it and removing waste substances cast off from it. The action of the waves in floating out the tangles of rockweed of the mid-littoral belt, and of then keeping them in almost constant motion, indicates that both a better aeration of the water and a higher rate of interchange of nutrient and waste substances between water and plant must result. These would be very interesting points to settle definitely by carefully checked physiological experiments.

The influence of water-movement on a plant may also be exercised secondarily through the favorable or unfavorable effect of this movement on its competitors. For example, it is evident that the inability of large sheets of *Ulva* to withstand the strong current in the Inlet prevents the huge sheets of this species from covering large areas of the bottom here, as it does in the quieter parts of the Inner Harbor, and thus prevents it from smothering out many of the species that now find congenial conditions in the Inlet. On the other hand, the drifting by the tide of the rolls of *Ulva* mentioned on page 20, and the final settling of these on patches of *Zostera* and *Ruppia*, may smother these latter out in the same way that the masses of *Ulva*, *Enteromorpha clathrata*, or of other tide-trash, have been shown to smother *Spartina glabra*, and the algal felts with it, in the mid-littoral belt. It is probable that it is the inability of other brackish-water algæ to gain, or maintain, a foothold in such a swift current that gives *Ilea fulvescens* such undisputed sway on the steeper pebbly bottoms of the Creek between 150 south and 500 south.

3. THE CHARACTER OF TIDAL CHANGES AND THEIR INFLUENCE ON PLANT DISTRIBUTION.

In the earlier sections we have repeatedly referred to various effects of the tidal changes in water-level on individual species of plants. We may now look more closely into the magnitude of the tidal changes in water-level and the ways in which the latter may affect the growth, and other physiological activities, of littoral plants, and thus aid in determining their distribution. These peculiarities and effects of the semi-daily rise and fall of the tide may be discussed under the following heads: (A) Characters of the Tides; (B) Effect of Tidal changes on Evaporation; (C) Effect on Aeration; (D) Effect on Salinity of Soil-Water at High Levels; (E) Effect on Exposure to Rain; (F) Effect on Light Supply.

In addition to the effects just enumerated the tides cause part of the water-currents that are referred to above and also have an influence on the salinity and the temperature of the water of the harbor in general, which are to be discussed below.

A. CHARACTER AND MAGNITUDE OF THE TIDES.

The predicted, semi-diurnal range in water-level, due to tides, varied during the growing season of 1911 from 4.2 feet to 10.8 feet. (See plate XXIV, and Tittman, 1910.) The "mean range" during this season was 7.63 feet. This mean range varies from year to year, and the one here given for the growing season of 1911 is about 0.1 foot below the "corrected mean range" for three or four decades.

The smaller or "neap range" occurs just after the first and third quarters of the moon in each month. This neap range varied, during the months from May to October 1911, from 4.2 feet on October 1 to 7.0 feet on June 20. The greater or "spring range" occurs just after the new moon and the full moon. This varied in 1911 from 8.5 feet on July 14 (and 8.6 feet on June 10) to 10.8 feet on May 27. (It was 10.7 feet on October 10 and even 11 feet on April 30, the day before the beginning of our somewhat arbitrarily fixed growing season.) These various facts are indicated graphically in plate XXIV. The chart there shown was constructed from data given in the U. S. Tide Tables above referred to. (See also tables A, B, and C, pp. 135, 136.)

Of course, the high water actually occurring at Cold Spring Harbor may sometimes be higher than that predicted, because of a northerly wind blowing the water into this long, narrow harbor. Or on another day high water may be lowered by a southerly wind retarding the inward flow of the water at flood-tide. On the other hand, the height of a low tide may be lowered by a strong southerly wind or kept above the predicted height by the retarding effect of a northerly wind during ebb tide. In the long run, however, this influence of the wind in modifying the water-level at high and at low tide would prove about equal in both directions, and so the actual tides would show an average or mean range corresponding closely with that of the predicted tides. It must be remembered that any effect of a general prevalence of winds from one direction, *e. g.*, from the southwest in summer, is one of the factors included in the actual tides observed at Cold Spring Harbor in 1894, on which observations the prediction of tides for this station is based.

The general effect of the semi-diurnal variation of water-level, with high and low tides, on the vegetation of the shores, is probably dependent (see p. 14

above) chiefly on the average or mean range of the tides from end to end of the growing season. For plants growing just below mean low water or just above mean high water it is probable that the occasional extremely low tides or extremely high tides may be of great, possibly of preponderating or critical, importance (see p. 15 above). We shall look into this latter question in more detail later on.

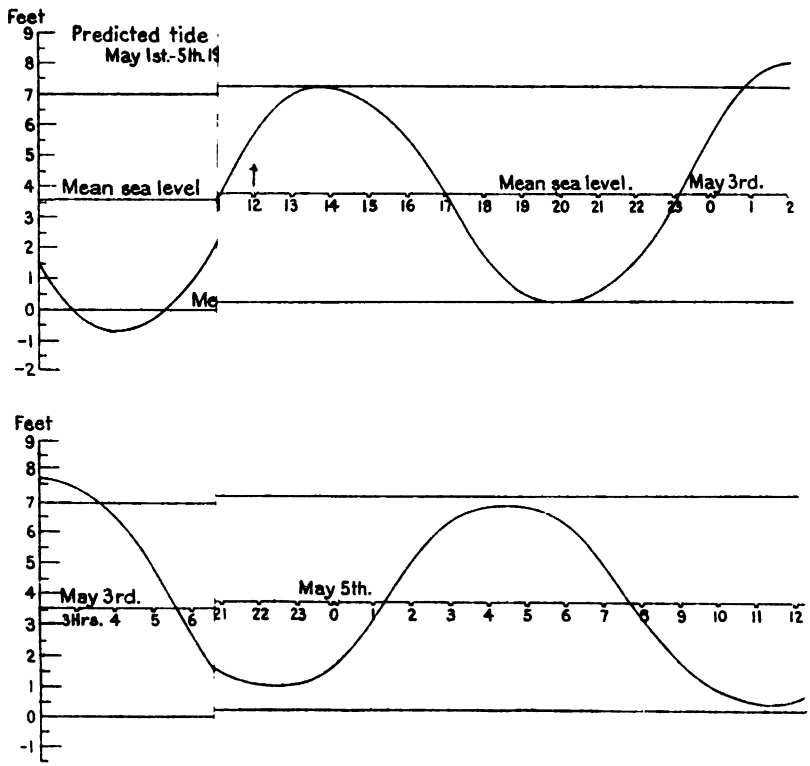
It is evident that the direct primary effect of this oscillation of the water-level, twice each "lunar day" of 24.9 hours, will be the twice repeated submergence by the water and exposure to the air of all plants growing between tide-marks. While the roots and submerged portions of the shoot are under water they are wholly or partially shut off from the light and completely shut off from a supply of air, except as this may be conveyed to them from the exposed portions or absorbed from the submerging water. The possible secondary effects of this submergence and exposure we shall attempt to analyze later on.

The determination of the exact time of submergence and exposure of soils and plants at the various levels necessitates carefully made and recorded observations of the rate of rise and fall of the tide. Since no such data for the Inner Harbor at Cold Spring Harbor were available, measurements were made in the manner described on pages 12 to 14 above. These measurements are expressed in the curve shown in plate VI, which was briefly described earlier in this paper (p. 13), in order that the data embodied in it might be used in the discussions in Section III.

The chart referred to gives the curve for two successive tides of a single lunar day. The tides chosen are of about mean range. From this chart the submergence and exposure, by an average tide, of all levels of the shore between mean low water and +7 feet, might be determined. But in order that the average submergence and exposure during the growing season of these levels, and of levels lower and higher than these, might be determined, records of all tides, from May to October, were needed. Since we were unable to make these by actual measurement at Cold Spring Harbor, recourse was had to the records of actual tides, and especially to the predicted tide curves, for Willet's Point, New York. This is the nearest tide-recording station of the U. S. Coast and Geodetic Survey and is the "standard port for reference" for Cold Spring Harbor. An actual recorded curve for Willet's Point for July 18, 1894, is shown in the chart in figure 4.[a] This shows the form of curve for a tide of mean range. This curve has the general form of that for the tide of mean range at Cold Spring Harbor, though it shows a slight flattening at the top, and a striking retardation in the rate of fall of the water-level just before mean low water is reached. Plate XXIII shows a portion of the "predicted tide curve" for May 1911, made by the tide-predicting machine of the Coast and Geodetic Survey.

In these predicted curves for tides at Willet's Point those for mean tides show a close resemblance to the curve of the actual mean tide at Cold Spring Harbor. We may, then, assume, what is highly probable, that the curves of actual tides of neap range and of spring range at Cold Spring Harbor would resemble in general those for the same tides at Willet's Point, just as the curves

[a] The writers are greatly indebted to Mr. O. H. Tittman, Superintendent of the Survey, for his kindness in having the curves of actual tides traced and in having the predicted curves, for the season from May 1 to October 31, 1911, made anew for us, by the new tide-predicting machine of the Survey.



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of actual mean tides at the former station were found to resemble those for the same tides at the latter station.[a]

If, then, we allow for the 0.4 foot greater height of high water at Cold Spring Harbor, we can, from this predicted curve for Willet's Point, determine with sufficient accuracy the probable duration of submergence and of exposure of any level between tide-marks at Cold Spring Harbor. That is, we can determine by measurement, between the points of intersection of the horizontal line representing any level with the curve, the submergence and exposure of that level per lunar day per month, and so the total for the whole season of six months.

Table A, page 135, gives the duration of submergence and emergence, per lunar day and per average calendar month, for various levels from —1.25 feet to +9.00 feet measured from this predicted curve. This table shows in the second and third columns the average total submergence in hours per month of each level. The emergence of levels below mean low water and the submergence

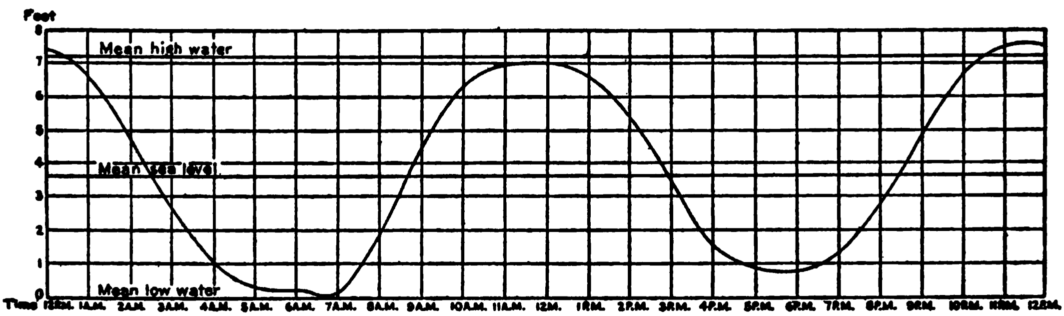


FIG. 4.—Chart of tidal-curve of two successive mean tides, recorded at Willet's Point, New York, on July 18, 1894 (supplied by the U. S. Coast and Geodetic Survey). (In comparing this curve with that in plate XIV note that the horizontal unit of the scale, representing an hour of time, is 20 per cent greater than the vertical unit, representing a foot in height, instead of equal to it, as in plate XIV. This accounts in part for the greater flattening of the crest and hollow of the curve.)

of levels above 6.5 feet was measured on the predicted curve for Willet's Point for all tides of the season. In determining the submergence and exposure of levels from 5 feet upward, allowance was made for the greater height of high water at Cold Spring Harbor, by measuring the submergence for each level at 0.4 feet lower down from the crest of the curve of the tide for that day, or by measuring it on the curve of a tide of proper height, though it happened to be on another day. The durations so obtained when divided by 6 give the average durations of submergence or emergence for each month of the growing season. The *submergence* of the *lower levels* was obtained by subtracting the total

[a] Actual records of the tides of the Inner Harbor at Cold Spring Harbor were made with a tide-gage loaned by the U. S. Coast and Geodetic Survey, in July, August, and September, 1913. The form of this curve corresponds very closely with the constructed curve shown in plate VI and with the predicted tide-curve for Willet's Point. The most striking peculiarity of the curve recorded at Cold Spring Harbor in 1913 is the sharpness of the trough at low water. This probably means that the times of emergence, given on page 136, for plants growing near mean low water are slightly too large.

monthly emergence from 736.5, the average total number of hours in each month. The *emergence* for the *higher levels* was obtained by subtracting the monthly submergence from the average number of hours in a month. The exposure of any level varies greatly, of course, from month to month. Thus, *e. g.*, the −1-foot level was not exposed at all in August 1911, while its probable emergence for May was 9.5 hours. Again, the probable submergence of the 8.75-foot level for August 1911 was 0.0 hours, while for May it was 11.25 hours.

The average monthly emergence of levels between mean low water and 3 feet was obtained by measurement on the predicted tide-curve for Willet's Point for August, since the mean low water for this month (0.038 foot) was closest to that for the whole six months of the growing season (0.006 foot). The submergence of levels between 4 feet and 6.5 feet was obtained by measurement on the predicted curve for June 1911, since the average high water for this month was exactly that for the season (7.63 feet).

The fourth and fifth columns of Table A show respectively the average emergence and submergence per lunar day of 24.88 hours, there being 29.6 lunar days per month, or 177.5 lunar days per growing-season. From these data, or those for the month, the total emergence or submergence for each of the 59 tides per month (average) or 355 tides per season can be obtained.

The sixth column of Table A gives the ratio of emergence to submergence for each level. These figures will be of value when discussing the upper and lower limits of plant distribution (see Section VI), since from them we can see the proportion of submergence to emergence endured by any plant at its upper or at its lower limit.

Another series of tidal data of interest in connection with plant distribution is that concerning the frequency of submergence or emergence respectively of levels near the upper margin and the lower margin of the littoral region. From the predicted heights of the low waters and of the high waters for each tide of the season, given in the United States Tide Tables for Cold Spring Harbor, it is possible to determine *exactly* the number of tides each month, or the total number per season, in which any level near high-water mark will probably be submerged, or any level near low-water mark will probably be exposed, the only uncertainty in these cases being the possible effect of the wind in making the level attained higher or lower than that predicted.

Table B (p. 136) shows the number of submergences per month and per season (May to October) of levels from 6 to 9 feet. These numbers were obtained directly from the Tide Tables by adding the 0.4-foot correction to the predicted high waters for Willet's Point for each tide of the growing season. In connection with these numbers it should be recalled that there are 355 tides per season, which includes 58 each for June and September, 59 for October, and 60 each for May, July, and August. From this table of infrequent submergences can be deduced the duration of the longer continuous emergences of these high levels.

Table C (p. 136) shows the number of emergences per month and per season of levels between −1.25 feet and +1.75 feet. These figures, like those in Table B, are taken from the heights of predicted low waters for Willet's Point, which are in this case identical with those for Cold Spring Harbor. From the

frequency of emergence of each level here given the duration of the longer submergences of these low levels can be obtained.

From Tables B and C it is evident that the −1-foot level and all below it may be continuously submerged for a month at a time, *e. g.*, during August. Even the 0-foot level may, as can be seen from the Tide Tables, be submerged continuously for from 4 days at a time, in May, to 7 days in June or August. On the other hand, the higher levels may be exposed continuously, never being wet by the tides, for many days together. Thus, *e. g.*, in 1911, the 8-foot level was continuously exposed for 10 days in June, or even 12 days in July. Even the 7.5-foot level may be exposed continuously for 4 days at a time, in June, or even 7 days, as from August 30 to September 6, 1911. For levels above 8 feet the duration of continuous exposure would evidently be markedly greater. These unusual tides which submerge the higher levels and expose the lower ones are grouped in two series each month, *i. e.*, at the two periods of spring tides. This fact is of great importance to the plants growing at these levels. It means that plants at the −1-foot level, *e. g.*, may be constantly submerged for a month at a time and then, after three or four periods of exposure, of from half an hour to an hour per tide, they may again remain submerged for a fortnight or a month. So far as enduring submergence is concerned, this is probably equivalent for the plant to constant submergence. The plant is, however, obliged occasionally to withstand the exposure to sun and wind. In fact, even such a brief exposure may be of critical importance in limiting the upward extension of a delicate species.

With so much of general discussion of the tidal changes themselves, we may now turn to take up their effect on plants.

TABLE A.—*Duration of submergence and exposure, from May 1 to October 31, 1911.*

Level.	Total emergence. Average per calendar month.	Total submergence. Average per calendar month.	Average emergence per lunar day.	Average submergence per lunar day.	Ratio. Emergence. / Submergence.
Feet.	*Hours.*	*Hours.*	*Hours.*	*Hours.*	
−1.25	1.66 [1]	734.84	0.06	24.82	1.66/734.84= 0.0023 [2]
−1.00	3.70 [3]	732.80	0.12	24.76	3.7 /733.0 = .0051
−0.50	23.50 [4]	713.00	0.79	24.09	23.5 /713.0 = .0316
0.00	53.70	682.80	1.82	23.06	53.7 /682.8 = .0788
+0.50	112.75	623.75	3.80	21.08	112.75/624.0 = .1791
+1.00	180.40	556.10	6.10	18.79	180.4 /556.0 = .3244
1.50	239.25	497.25	8.08	16.80	239.2 /497.2 = .4807
2.00	261.25	475.25	8.83	15.95	261.2 /475.2 = .5500
3.00	338.75	397.75	11.07	13.81	338.7 /397.7 = .852
4.00	397.50	339.00 [6]	13.43	11.45	397.5 /339.0 = 1.172
5.00	461.50	275.00	15.59	9.29	461.5 /275.0 = 1.674
6.00	533.62	202.88	18.03	6.85	533.62/202.88= 2.625
6.25	559.50	177.00	18.55	6.33	559.5 /177.0 = 3.161
6.50	575.50	161.00	19.44	5.44	575.5 /161.0 = 3.574
6.75	601.50	135.00	20.32	4.56	601.5 /135.0 = 4.455
7.00	639.50	97.00	21.27	2.67	639.5 / 97.0 = 6.593
7.50	689.30	47.20	23.28	1.60	689.3 / 47.2 = 14.60
8.00	706.14	30.36 [7]	23.86	1.02	706.1 / 30.4 = 23.26
8.25	719.70	16.83	24.31	.57	719.7 / 16.83= 42.76
8.50	727.80	8.70	24.59	.29	727.8 / 8.7 = 83.65
8.75	731.86	4.64	24.73	.16	731.86/ 4.64=157 51
9.00	734.42	2.08	24.81	.07	734.42/ 2.08=353.09 [5]

[1] Max. 5.5; min. 0.0.
[2] This means that this level is exposed only $\frac{1}{433}$ as long as it is submerged.
[3] Max. 9.5; min. 5.0.
[4] Max. 34.50; min. 12.5.
[5] This means that this level is exposed 353 times as long as it is submerged.
[6] June. [7] Season.

TABLE B.—*Number of submergences per calendar month and for the season, from May 1 to October 31, 1911.*

[In each column, under the name of the month (or the season), the figures give the number of times that the level in question is submerged during that month or during the season.]

Level.	May. (60 tides.)	June. (58 tides.)	July. (60 tides.)	Aug. (60 tides.)	Sept. (58 tides.)	Oct. (59 tides.)	Season. (355 tides.)
Feet.	*Times.*	*Times.*	*Times.*	*Times.*	*Times.*	*Times.*	*Times.*
6.00	60	58	60	60	55	58	351
6.25	60	58	60	56	52	57	342
6.50	60	58	60	54	52	53	337
6.75	59	58	54	51	43	46	311
7.00	52	54	52	44	43	39	284
7.25	39	39	44	37	37	33	229
7.50	33	33	38	34	32	30	200
7.75	26	24	28	28	26	23	155
8.00	23	14	21	22	21	20	121
8.25	11	7	6	12	15	14	65
8.50	8	5	3	2	5	7	30
8.75	7	4	0	0	3	4	18
9.00	5	0	0	0	1	4	10

TABLE C.—*Number of exposures per calendar month and for the season, from May 1 to October 31, 1911, of levels from—1.25 feet to 1.75 feet.*

Level.	May. (60 tides.)	June. (58 tides.)	July. (60 tides.)	Aug. (60 tides.)	Sept. (58 tides.)	Oct. (59 tides.)	Season. (355 tides.)
Feet.	*Times.*	*Times.*	*Times.*	*Times.*	*Times.*	*Times.*	*Times.*
−1.25	5	1	0	0	0	3	9
−1.00	5	3	2	0	3	4	17
− .50	16	9	6	14	17	17	79
0.00	29	26	27	28	28	27	165
+ .50	45	48	52	43	40	36	264
+1.00	56	58	60	55	48	46	323
1.25	60	58	60	59	53	53	342
1.50	60	58	60	60	55	55	348
1.75	60	58	60	60	58	59	355

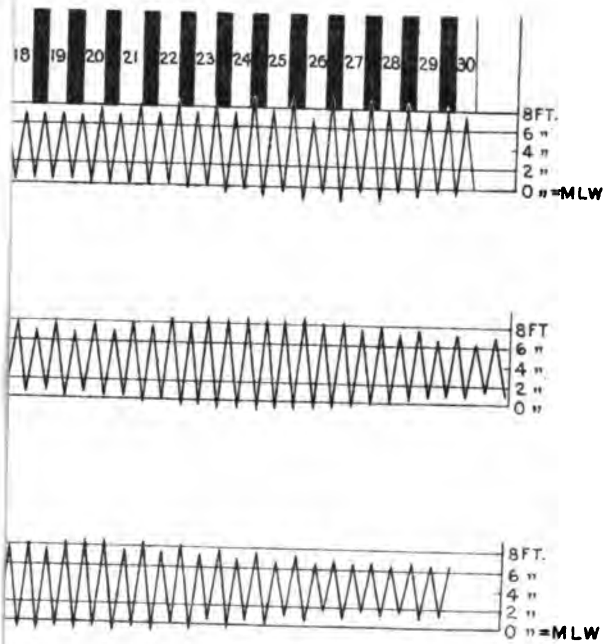
B. EFFECT OF TIDAL CHANGES IN WATER-LEVEL ON EVAPORATION OR TRANSPIRATION FROM THE PLANT.

It is, in the first place, clear that when delicate, thin-cuticled plants like *Zostera* or *Ulva* are exposed at low tide during a warm, sunny day, they may be subjected to a dangerous desiccation. This desiccation, to which plants growing above mean low water are liable, is undoubtedly concerned with determining the upper limit of distribution of such species.

As has been mentioned in Section III, many plants of *Cladophora, Enteromorpha,* and *Ulva,* of various red seaweeds, and the leaves of *Zostera,* are often killed off by drying out on hot days in summer. The *Ulva* is oftenest destroyed by being floated to the higher levels of the beach by the air bubbles that collect under it on a hot day.

We have spoken also (p. 91) of the drying out, and cracking to polygonal, tile-like blocks, of the felts of Schizophyceæ and Chlorophyceæ occurring on the south shore of the Spit, between the 6.5 and 7.5 foot levels. At slightly higher levels these felts are usually wanting, probably chiefly because they and the soil bearing them are less frequently wet by the high tides, but are exposed to desiccation for a longer time. That the relative dryness of these higher levels really determines the absence of these algal felts seems clearly indicated by the fact that these felts may occur above their usual level when on the north or shady side of tufts of grasses, *e. g.,* at 7.5 to 8 feet, on the top of the stone pier on the eastern shore.

PLATE XXIV.



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For the algæ growing on the vertical stone walls and piles of the wharves, also, the upper limit of distribution is evidently determined by the amount of desiccation the plants can withstand. We have seen, *e. g.*, (pp. 65 and 67) that *Rhizoclonium* and *Fucus* go highest in crevices in the wharf, or on the north sides of piles, where not reached by the sun and by winds.

In like manner, for erect-growing seed plants between tide-marks, like *Spartina glabra,* the elevation attained is evidently conditioned, at least in part, by the desiccation it is subjected to. That is, by the length of time at each tide that its leaves are exposed to the dry air. A clear indication that this is the case is found in the fact that on certain shaded areas with moist soil on the western shore, this grass grows at a level much above its usual upper limit. It displaces here its sun-loving competitor *Scirpus americanus,* which as usual holds sway at these higher levels on adjoining dry and sunny portions of the shore. That a grass with rather thick-cuticled, rolling leaves should be endangered by the amount of transpiration it can be subjected to just above the 6.5-foot level, while its rhizomes and roots are embedded in a practically saturated soil, seems surprising at first thought. But it is to be remembered that the humidity of the air about the upper half of the plant, which includes most of the well-developed leaves, may be quite low. This is especially true of the south shore of the Spit, which is just where the upper boundary of the *Spartina* is strikingly definite.

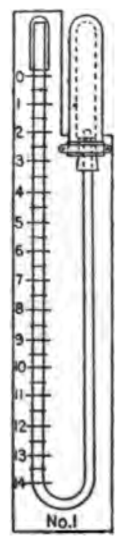

FIG. 5. Atmometer used between tide-marks.

That attempt was made to determine the evaporating power of the air in this habitat of *Spartina* on the Spit, and in several other typical habitats by means of a porous-cup atmometer. For this purpose three atmometers were used, whose coefficients of correction had been determined by comparison with a Livingston standard atmometer. All the readings here given are corrected readings, and may therefore be directly compared with the Livingston standard.

For use at levels where, because of the danger of submergence by the tides, exposures can be made for only a few hours at a time, except occasionally during a series of neap-tides, an atmometer is required which will indicate very small losses of water. For this purpose the porous cup was attached to the shorter arm of a U-tube, the other arm of which was graduated to tenths of a centimeter by filling from a burette. The resulting instrument (fig. 5) is a simplified form of that described by Livingston 1906. Three instruments of this kind, which we will designate as Nos. 1, 2, and 3, were run simultaneously for a week in an instrument shelter, to discover possible leaks and to check up their relative rates.

For three days in August 1909, during a series of neap tides, the three atmometers were exposed in different places and simultaneous readings made at the beginning and the end of each of the following periods: August 6, 11^h00^m a. m. to 12^h40^m p. m.; August 7, 7^h20^m a. m. to 12^h20^m p. m., and August 7, 12^h20^m p. m. to August 8, 7^h30^m a. m. The total exposure for each instrument was 25.8 hours. The days on which the exposures were made were clear. The temperature recorded by a Friez thermograph in the shelter ranged from 18°

to 30° C., while the humidity recorded by a Friez hygrograph in the same place varied from 50 to 95 per cent. Atmometer No. 1, in the shelter, showed an average corrected rate of loss of 0.43 c. c. per hour. It showed a minimum rate of 0.37 c. c. per hour in the period from 12^h20^m p. m. August 7, to 7^h30^m a. m. on August 8, when the temperature ranged from 18° to 30° C., averaging 23.5° C., and the humidity ranged from 50 to 95 per cent, averaging 79 per cent. The maximum rate for this instrument of 0.75 c. c. per hour was shown on August 7 from 7^h20^m a. m. to 12^h20^m p. m., when the temperature ranged from 21° to 27° C., averaging 22.2°, and the humidity varied from 53 to 75 per cent, averaging 69 per cent.

Atmometer No. 2, placed in a dense stand of *Spartina glabra* at 2,750 north by 290 east, with its cup at the 7.5-foot level and about 1.5 feet above the soil, gave an average corrected rate for the whole 25.8 hours of 0.79 c. c. per hour. The minimum rate at this station was shown for the period from August 7, 12^h20^m p. m. to August 8, 7^h30^m a. m., the temperature and humidity in the shelter for this period being those given above. This corrected minimum rate was 0.67 c. c. per hour. The maximum rate for No. 2 of 1.1 c. c. per hour was also shown in the same period and under the same conditions as the maximum for No. 1, *i. e.*, on August 7, from 7^h20^m a. m. to 12^h20^m p. m.

Atmometer No. 3 was placed 10 feet south of No. 2 among the stems of *Spartina*, in a reclining position, with its cup 4 inches above the soil and at about the 6.3-foot level. The corrected rate of this instrument varied from 0.36 c. c. per hour to 0.63 c. c. It is interesting to note that the relative rate of this instrument varied from 0.5 to 1.7 times that of No. 1. This wide difference in rate of two instruments exposed simultaneously is probably due to the differences at the station for No. 3 in the direction and strength of the wind, and especially to the different amounts of water, from the preceding high tide, left clinging to the *Spartina* stalks at the beginning of the exposure.

The amount of this adhering water would depend on the length of time since the tide receded from that level; also on the temperature and on the direction and strength of the wind, which might dry it off. It must be borne in mind, however, that the variations in evaporating power of the air here mentioned are entirely characteristic of locations between tide-marks, and are therefore real factors in the environment of plants, which, like the algæ on the mud and on stalks of the *Spartina*, live in these habitats.

Another series of records was made in which atmometer No. 1 was placed in the shelter, No. 2 was placed on the vertical stone wall, facing east, at 200 north by 80 west, near the 6.5-foot level, and thus near the upper edge of the rockweed belt, and No. 3 was placed at this same level on the north-facing wall at 10 south by 40 east. The three atmometers were exposed simultaneously during a total of 32.7 hours of daylight from July 27 to 30, 1909, in clear weather, while the temperature ranged from 22.8° to 34.4° C. (averaging 28° C.), and the humidity varied from 39 to 87 per cent (averaging 60 per cent).

The record of No. 1 under these conditions showed an average corrected rate of 1.08 c. c. per hour (ranging from 0.89 to 1.56 c. c. per hour); No. 2 gave an average rate of 0.9 c. c. per hour (ranging from 0.5 to 1.16 c. c. per hour); while in No. 3 the rate averaged 0.72 c. c. per hour (ranging from 0.59 to 1.14 c. c. per hour).

Other series of atmometer records were started, but, because of accidents or lack of time, were not made complete enough to be of significance.

From what has been said it is evident that the maximum rate of evaporation of 1.1 c. c. per hour recorded in the middle of a moderately warm day, by an atmometer among the leaves of the *Spartina glabra,* indicates that these plants are at times subjected to a relatively high rate of evaporation. If we multiply this hourly rate by 168 we get a weekly rate, 185, that closely approaches the highest average weekly evaporation-rate, for the growing-season, in the United States east of the Mississippi, given by Livingston (1911, p. 219). Even the average hourly rate for atmometer No. 2 in the *Spartina,* which included one night in the total exposure of 25.8 hours, was 0.79 c. c. per hour, or 133 c. c. per week. This considerably exceeds the average weekly evaporation for the summer at New York City, as given by Livingston (1911, p. 213), and the weekly rate of 95.5 c. c. at 2 meters above the soil found by Fuller (1912, p. 426) in a mesophytic beech-maple forest of Indiana. In fact, it very closely approaches that given for Salt Lake City (Livingston, p. 210). It nearly equals also the average rate of 0.83 c. c. per hour given by Transeau (1908, p. 219) for his standard instrument, established in an open garden at Cold Spring Harbor. The rate of atmometer No. 2 in the *Spartina* for the period that included the afternoon and the night of August 7, was 0.67 c. c. per hour or 113 c. c. per week. This indicates the correctness of Transeau's suggestion (1908, p. 227) that the low average rate of evaporation from his atmometer, placed at the 12-foot level, on top of the Spit, in 1907, was due to the very slight evaporation occurring there at night.

The rate of instrument No. 2, when placed on the wall of the wharf, amid the rockweed, against stones saturated by water, and only 5 feet above the muddy bottom, with its trickling rivulets, averaged 1.08 c. c. per hour, or 181.5 c. c. per week, while its maximum rate reached 195 c. c. per week. This indicates the high rate of evaporation to which the rockweeds, *Rhizoclonium, Bostrychia,* and the Schizophyceæ of the wharves may be subjected, during low tide. These rates in fact approach the rate for the area about Lake Erie (200 c. c. per week), which is the highest average weekly evaporation-rate given by Livingston (1911, p. 219) for any part of the United States east of Texas or the Dakotas.

It is, of course, realized that the few atmometer records here given can be considered adequate to do little more than indicate the importance of this evaporation-rate as a feature of the environment of shore-plants living between tide-marks. To get a really adequate idea of the importance of this factor in the environment of plants growing at any level, we must have records by quick-registering atmometers exposed at that level from the moment it is bared by the falling tide until it is just about to be covered by the rising tide. Moreover, readings must be made each hour or half hour of all exposures, night and day, from end to end of the season. When this is done, as it is hoped it may be soon at Cold Spring Harbor, it is believed that both the average rate, and, in some cases especially, the maximum rate of evaporation in their habitats will be found to be intimately concerned in determining the upper limit of distribution attained by many of the species growing between tide-marks.

C. EFFECT OF TIDAL CHANGES ON AERATION.

It is pretty certain that for thick-cuticled plants like the *Spartina, Distichlis, Salicornia, Suæda,* etc., the period of submergence at high tide is one during which there can be little interchange of gases between these plants and the surrounding medium. At this time the stomata of the shoot are closed by water and, during the whole time of submergence, the only supply of O and CO_2 available for the plant is probably that held in the air-canals of the shoot. In the case of *Spartina glabra* this stored supply occupies a considerable portion of the bulk of the shoot. The whole system of subterranean rhizomes and roots of these plants is dependent chiefly on the shoot for its supply of gases, since the heavy, fine-grained mud in which the rhizomes and roots, *e. g.,* of *Spartina glabra* are embedded is practically impenetrable to gases, except along burrows of the fiddler crab (*Gelasimus pugilator*) or those of the muskrat (*Fiber zibethicus*). Of course, except at spring tides, the upper portions of the leaves of the higher plants of *Spartina glabra* will still be exposed at high water, and it is possible that, by means of the abundant air-canals, gases may be exchanged between all parts of the plant and the outside air.

For the other species mentioned above, since they grow higher up on the shore, the air-supply is not cut off for so considerable a time as for *Spartina glabra,* though this deprivation must still be of some consequence, since such a plant, *e. g.,* as *Salicornia,* will, on the average, be more or less completely submerged for from one-fifth to one-third the daylight hours of an average summer day.

The effect of submergence on the physiological activities of such plants could probably best be determined by growing them in a tide-pond the level of which could be maintained at a constant level for any time desired.

For seed plants like *Zostera* and *Ruppia,* whose upper limit is not far above mean low water, it is probable that the necessary gaseous interchange is accomplished during submergence, through the thin-walled epidermal cells. The same thing is perhaps largely true for the algæ growing between tide-marks. Most of these, *e. g.,* the rockweeds, *Rhizoclonium,* and the Schizophyceæ, have more or less gelatinous cell-walls, which quickly dry on exposure and so form a nearly impermeable membrane over the surface. On many days, it is true, only the outer exposed branches of *Fucus* or *Ascophyllum* and perhaps of other algæ become really dry on the surface. Hence there may be a considerable gaseous interchange occurring even during low tide, a point which can be certainly determined only by experiment.

D. EFFECT OF TIDAL CHANGES ON SALINITY OF SOIL-WATER AT HIGHER LEVELS.

One of the effects of tidal changes may be that of periodically increasing the salinity of the soil-water. Near the 8-foot level, *e. g.,* are certain areas where, during neap tides, the soil is barely moistened by slowly seeping fresh water, but at the fortnightly spring tides the salinity of the soil-water of these areas is increased by the salt brought up by the high tides. The effect in these cases is probably not large. In the case of the fresh-water tributaries of the harbor, the change in salt-content with tides of varying height is probably much more important. For example, there are growing in the larger streams, between the 6-foot and 8-foot levels, algæ such as *Ilea* and *Enteromorpha,* which may be

surrounded by pure fresh water continuously for 10 days and then, during 5 or 6 days of spring tides, be subjected to strongly saline water for from 1 to 2 hours at each high tide. As was suggested earlier, the effect of this submergence is probably not great, except on soils that are comparatively dry in the intervals between series of spring tides, since in wet soils the salt water occasionally flooding them probably does not penetrate far.

On dry shores, however, there is a strip of soil between the 7.5 and 8.5 foot levels where the salt-content is probably increased during each series of neap tides. This may be brought about by the constant movement upward of the water in the soil by capillarity to levels above that of the high water of the neap tides. By the evaporation of the water from the soil the salt will continue to accumulate at the levels mentioned until the soil is flushed out by the high waters of the spring tides, or by rains.

E. EFFECT OF TIDAL CHANGES IN EXPOSING PLANTS TO RAIN.

On the effect of tidal changes in exposing plants to rain there are but few observations to record. It is evident that all shore and bottom plants above —1 foot may be subjected to a pretty thorough washing with fresh water by any heavy rain of the growing season that occurs during low tide. Many of these plants, like *Spartina* and the rockweeds, may be drenched with rain for 6 or 8 hours at a time and not suffer from it. We have noted above that *Fucus* and *Ascophyllum* may lie for several hours in pure fresh water at low tide. In the case of certain of the red seaweeds, however, such as the *Ceramiums* on the *Zostera*, and plants of *Agardhiella, Chondria,* and *Polysiphonia,* a drenching of this sort, especially if followed by exposure to a hot sun, may cause the death of the plant. Large portions of the great sheets of *Ulva* are frequently found dead after exposure to such conditions.

In general, all observations thus far made seem to show that nearly all the plants found above mean low water may withstand a more or less protracted wetting with fresh water, though only a few like *Ilea, Enteromorpha intestinalis,* and *Ectocarpus* do, as we have seen in Section III, actually live where subjected to this every day.

F. EFFECT OF TIDAL CHANGES ON THE LIGHT-REACHING PLANTS.

It is evident that even in clear water the effective solar energy reaching submerged plants or parts of plants is markedly lessened by each foot of water it must pass through. In water of the turbidity of that often found along the shores of our harbor it is probable that submergence of a plant in 2 feet or, sometimes, even in 1 foot of water will practically put a stop to photosynthetic activity. In the middle of the harbor the water is usually less turbid. In fact, on real quiet days it may be very clear at and near low water.

From what has just been said it is evident that plants growing below high-water mark must do most of their photosynthesis during low tide. A reference to plate XXIV will show that since, on half the days of each month, high water occurs near the middle of the day (*i. e.,* between 9 a. m. and 3 p. m.), it is evident that the most effective sunlight is, on these days, cut off from plants below high-water level for a longer or shorter time. This would be most markedly true of plants nearer low-water mark, but still true in some degree of all plants below

high-water mark. All these facts taken together show that for a plant growing, say, at the 4-foot level (*i. e.,* near mean sea-level), the time for the most effective photosynthetic work, that is, the total duration per month of emergence during brightest daylight (9 a. m. to 3 p. m.) is reduced to about one-half that for a plant growing in the open, above high-tide level. In other words, while the exposure of an upland plant would be 6 hours in the middle of the day, that for plants at mean sea-level will vary from 0.25 to 6 hours per day, averaging 3 hours per day for the month or season. Since the 4-foot level mentioned is about the average level of the photosynthetically active leaves of the lowest plants of *Spartina glabra* we have, in the 3 hours' exposure mentioned, the approximate light minimum endured by this grass. Just what part this reduced lighting may play in determining the lower limit of distribution is uncertain. Plants which are left submerged for a longer time than this by planting them at mean low water on the harbor bottom die out in one season. The effects of the various factors that are changed by this longer submergence can only be distinguished and determined by more prolonged experimental work than we have yet been able to carry out.

The above given proportions, of light-reaching plants at different levels, were determined from the predicted tide-curves for Willet's Point, New York, from May 1 to October 31, 1911, which are described on page 131 above. This curve for Willet's Point is the closest approximation to that for Cold Spring Harbor that can be obtained, the chief difference in the two being the 0.4 foot greater height of high water, which would tend to slightly decrease the time of lighting of levels from mean sea-level upward. Table D gives the times of exposure per day of four selected levels to total daylight, *i. e.,* from sunrise to sunset, and to brightest light, *i. e.,* from 9 a. m. to 3 p. m., for the month of May 1911, determined from the above-mentioned predicted tide-curve.

TABLE D.—*Daily exposure of various tide-levels to daylight.*

Level.	Exposure to total daylight.			Exposure between 9 a. m. and 3 p. m.		
	Range in exposure per day.		Average exposure per day.	Range of exposure per day.		Average exposure per day.
	Minimum.	Maximum.		Minimum.	Maximum.	
	Hours.	*Hours.*	*Hours.*	*Hours.*	*Hours.*	*Hours.*
9 feet (and above)..	13.96	14.98	14.50	6.00	6.00	6.00
7 feet..............	12.35	14.68	14.02	4.00	6.00	5.54
3.6 feet...........	6.2	9.15	7.7	0.15	6.00	3.00
0.0 foot...........	0.0	5.60	1.5	0.0	1.25	0.12

It is interesting to note here that the 0.0-foot level may not be exposed at all to daylight for 8 days at a time, and not be exposed at all between 9 a. m. and 3 p. m. for 25 days out of the month. In this connection, however, we must recall again the often great clearness of the water in the center of the harbor at low tide, which allows plants at and below this level to get rather intense light at low water, even though submerged by a foot or more of water. Since in the case of *extreme* spring tides high water always occurs in the middle of the day, the 9-foot level, if submerged at all, is covered between 9 a. m. and 3 p. m., the hours of brightest daylight.

It is evident that the habitat of the lower plants of *Spartina glabra* really resembles that of shade plants, so far as light supply and moisture conditions are concerned. Though they do not show very striking differences in structure when compared with plants of the same species growing near its upper limit, some differences are discoverable. For example, the plants at the 2-foot level have weaker stalks, thinner and narrower leaves, thinner cuticle and less-developed photosynthetic tissue than plants at the 6-foot level. Of course, many plants growing at and below mean low-water level are decidedly like shade plants in many respects, as has been suggested by Warming (1909, p. 150). For example, *Zostera* and *Ruppia* have the attenuated form characteristic of plants etiolated by shade. In the case of the algæ *Ulva, Enteromorpha, Cladophora,* etc., found near low-water mark the structure is not markedly different, so far as was noted, from that of the same species at the highest levels these attain, except that the latter are smaller (perhaps we may say more stunted in growth). This is probably due to the fact that plants on piles and wharves at higher levels are more likely to be torn with the fall of the tide than are plants that lie on the bottom. A careful statistical study of the size of plants, of their cells, or the thickness of their cell-walls, might show constant differences in plants at different levels not hitherto detected. On the other hand, plants at the 7-foot level may get the maximum exposure of 6 hours per day to brightest daylight on 24 days of the month and lose an hour and a half or more of this light on only 4 days per month. Thus plants like *Spartina patens, Distichlis, Salicornia,* and *Suæda,* growing between 6.5 and 7.5 feet, are probably not much affected by the relatively small proportion of total daylight lost by submergence.

The general conclusion must be, then, that the shortened light supply of plants subject to daily submergence must affect their physiology, their structure, and hence their possible vertical range, in a very considerable degree, especially if they grow at or below mean sea-level. The exact effect of different exposures to light on different species of these plants has yet to be determined experimentally.

In summary of the various effects of tidal changes on plants, we find that these are of most general importance in affecting, first, the amount of transpiration; second, the time available for gaseous interchange between the shoots and the air; and, finally in limiting the light-supply and hence the effective photospnthetic activity of littoral plants. Of secondary and only occasional importance are the effects on concentration of the soil-water at high levels, and the exposure of plants near mean low water to rains during low tides.

4. THE SALINITY OF THE WATER OF THE HARBOR.

The normal specific gravity of the water near the surface of the harbor, at high water, was found to be 1.022 (at 15° C.). The salinity, and so the specific gravity, varies somewhat with the state of the tide, and may become much lower than 1.022 at low water. This lowering of the specific gravity is evidently due to the large admixture of fresh water from tributary streams and springs. The inflow of this fresh water remains constant, except that from springs between tide-marks, while the volume of water in the harbor with which this is mixed decreases very rapidly with the falling of the tide. The cubic contents of the harbor at high water is about 42,000,000 cubic feet, while at mean low water

Table E.—*Vertical distribu*

COMPOSITION OF V

Tide Levels.	Vegetational Belts.	Thallophytes.			
		Supra-Littoral Beach.		Supra-Littoral Marsh.	
12 feet.		Species.	Range.*	Species.	Ran
11 feet.	Supra-Littoral Belt. 8 to 12 feet. (Storm Beach and Supra-Littoral Marsh.)	Cladonia sp.	9 to 12	s Lyngbya sp.	8 to
				s Nostoc sp.	8.5
10 feet.					
9 feet.					
8 feet.					
	Upper Littoral Belt. 6.5 to 8 feet. (On all shores.)	c Rhizoclonium tortuosum			2 to
		s Calothrix (4 sp.)			6
		s Microcoleus chthonoplastes			4
		c Vaucheria sp			5
		c Enteromorpha intestinalis			0
7 feet.		s Lyngbya (8 sp.)			2
		c Ilea fulvescens			1.5
		c Monostroma latissimum			2.5
6.5 feet.		s Spirulina tenuissima			0
6 feet.	Mid-littoral Belt. 1.5 to 6.5 feet. Mid-littoral Marsh and Mid-littoral Rockweed Association.	p Ascophyllum nodosum			−1 to
		p Fucus vesiculosus			0
		p Fucus vesiculosus spiralis			1.5
		c Rhizoclonium tortuosum			2
		c Rhizoclonium riparium			6
		f Bostrychia rivularis			3
5 feet.		c Ulothrix flacca			3
		s Anabæna torulosa			4
		s Lyngbya æstuarii			4
		s Microcoleus chthonoplastes			4
		p Ralfsia clavata			?
		r Hildenbrandia prototypus			−1
		c Enteromorpha intestinalis			0
4 feet.		c Monostroma latissimum			2.5
		c Ilea fulvescens			1.5
		c Vaucheria sp			5
		c Cladophora expansa			4
		p Pylaiella littoralis robustus			−1.5
		r Delesseria leprieurii			1
3 feet.		s Rivularia atra			5
		r Porphyra laciniata			0
2 feet.					
1.5 feet.					
1 foot.	Bottom Vegetation. −5 to +1.5 feet. (Lower Littoral and Sub-littoral Belts.)				
		c Ulva lactuca latissima			−5 to
		c Enteromorpha clathrata			−1
		c Enteromorpha intestinalis			0
0 foot = M. L. W.		p Ascophyllum nodosum			−1
		p Fucus vesiculosus			0
		r Porphyra laciniata			0
		r Ceramium rubrum			−2
		r Ceramium strictum			−2
		p Pylaiella littoralis robustus			−1.5
−1 foot.		r Chondrus crispus			−2
		p Ectocarpus confervoides			0
		r Hildenbrandia prototypus			−1
		r Agardhiella tenera			−1
		s Spirulina tenuissima			0
		r Delesseria leprieurii			1
−2 feet.		Melosira nummuloides			−1
		Navicula grevillei			−1
−3 feet.					

* The two numbers given under "range" indicate the levels (above mean low water) between which the specie

The small letter before the name of each species shows to the eye, in glancing down the column, the phylo

s = Schizophyceæ, d = Dicotyledoneæ, and m = Monocotyledoneæ.

...ution of more common plants.

...OF VEGETATIONAL BELTS.

...	Cormophytes.			
...Limit...	Supra-Littoral Beach of Spit.		Supra-Littoral Marsh.	
...Range.*	Species.	Range.*	Species.	Range.*
	m Ammophila arenaria	8.3 to 12	*m* Scirpus americanus	6.5 to 12
	d Oakile edentula	8.5 11.5	Aspidium thelypteris	8.5 12
	d Solidago sempervirens	8 11.5	*m* Juncus Gerardi	7.3 8.8
	d Lathyrus maritimus	10 11	*m* Spartina patens	6.5 8.7
...5 to ?	*d* Euphorbia polygonifolia	8.5 12	*m* Eleocharis olivacea	8.3 12
	d Salsola kali	8.5 12	*m* Scirpus robustus	6.8 8.7
...5 ?	*d* Xanthium echinatum	10 11.5	*d* Solidago sempervirens	6.5 12
	d Aster tenuifolius	9 11	*d* Iva oraria	7.5 8.5
	d Atriplex arenaria	6.5 8.7	*d* Aster subulatus	7.3 9
	d Rhus toxicodendron	9 12	*d* Hibiscus moscheutos	8 12
	d Rhus glabra	11 12	*d* Gerardia maritima	8 8.7
	d Polygonum scandens	9 12	*m* Distichlis spicata	6.5 8.5
	d Ailanthus glandulosa	9 12	*d* Lysimachia terrestris	9 ?
	d Verbascum thapsus	9 12	*d* Asclepias incarnata pulch.	8.3 12
	m Agropyron repens	8.3 12	*m* Agropyron repens	8.7 12
	d Galium claytoni	8 12	Solaginella apus	9 12
	d Oenothera biennis	11 12	Pallavicinia lyellii	9 12
	d Robinia Pseudo-Acacia	9 12		
	d Salix sp	11.8 12		
	d Polygonella articulata	10 12		
...to 8	*m* Spartina patens	6.5 to 8.7	*d* Atriplex patula hastata	6 to 8.5
8	*d* Suæda maritima	6.5 8	*d* Limonium carolinianum	7.3 8.3
7.5	*d* Salicornia europæa	6.5 7.5	*d* Plantago decipiens	6.8 8.3
7	*m* Juncus Gerardi	7.3 8.8	*m* Scirpus nanus	6.8 8
7.25	*m* Scirpus americanus	6.5 12	*m* Triglochin maritima	6.3 7.5
7.5	*m* Scirpus robustus	6.8 8.7	*m* Typha angustifolia	7.8 12
...5 7.5	*m* Distichlis spicata	6.5 8.5		
...5 7.5	*d* Salicornia ambigua	6 7.5		
7	*d* Spergularia marina	7 8		
...to 7				
7.25	*m* Spartina glabra alterniflora			1.5 to 6.5
...5 6				
8				
7.5	*d* Lilæopsis lineata			5.5 6.5
7				
6.5				
7				
7				
7.5				
5				
7				
7.25				
...5 7.5				
...5 7.5				
7				
7				
...5 4.5				
5				
6				
4				
...to 4				
7				
7.25	*m* Zostera marina			−3 to 1.5
7				
7.25				
4	*m* Ruppia maritima			0 1
1.5				
1.5				
...5 4.5				
0				
2				
7				
1.5				
7				
5				
6.5				
1				

...pecies usually grows. The species are given in each belt in the order of prevalence.

...ylogenetic relationship of the forms of each belt. Thus: *c* = Chlorophyceæ, *p* = Phæophyceæ, *r* = Rhodophyceæ,

this is reduced to about 2,250,000 cubic feet, and at a low water of −1-foot, during spring tides, the volume may be only 700,000 cubic feet, or one-sixtieth of that at high water.

There is no adequate evidence that these variations in salinity are of consequence to the plants found established in the harbor. The low salinity at low water, however, may well be an important factor in preventing other red algæ, now occurring in the Outer Harbor, from getting a foothold in the Inner Harbor.

Of far more importance are the relatively rapid changes from water of a specific gravity of 1.019 to absolutely fresh water, and the reverse, to which plants growing between tide-lines in the fresh-water tributaries are subjected twice each day. We have already spoken of the algæ *Enteromorpha intestinalis*, *Ilea*, and *Monostroma* as occurring in or near fresh-water tributaries, where at high water they are surrounded by salt water, but, with the fall of the tide, are left with fresh water running over them, often for 8 or 10 hours continuously. The transition from one extreme to the other may, in the case of the small rivulets, occur very suddenly, probably in the course of a very few minutes. This is true because where there is but a small flow from a rivulet it may cause little mingling of the fresh and salt water about the algæ until the water has fallen almost to their level. Up to this time the fresh water, being lighter, simply spreads out on top of the salt water and leaves the algæ, which may be but an inch or two below, surrounded by salt water. Even in the case of larger streams such as that entering the harbor from the ponds of the New York State Fish Hatchery at 600 south by 720 east, Miss Streeter found that the water at the bottom, surrounding the algæ, may change from a specific gravity of 1.014 to one of 1.000 in an hour's time, with a fall of but 1 foot in the tide.

From a careful study of the floras of the between-tides portions of fresh-water tributaries, all about the harbor, it is evident that the rapid changes in salinity of the water must prevent many plants found elsewhere from growing in these areas. On the other hand, the ability of the algæ mentioned to withstand these conditions make these areas places of refuge for these algæ, where they are free from the competition of other species; *Ilea*, *e. g.*, for example, covers many square meters of the pebbly bottom of the Creek, between 200 and 500 south, practically to the exclusion of other species, except the inconspicuous diatoms. It must also be recalled that these rivulets have another advantage, perhaps the principal one, in that they form habitats where these more delicate algæ are not subject to desiccation during low tide, as they would be elsewhere at the same levels.

The salinity of the soil-water on various portions of beach and marsh, both at the same and at different levels, is undoubtedly a factor of very great importance in determining the distribution of plants. Reference has been made in the body of the paper to the fact that *Lilæa subulata*, *Scirpus americanus*, and *S. robustus* are found chiefly in soils more or less saturated with fresh water, and to the fact that *Iris versicolor*, and probably *Hibiscus moscheutos*, push down to their lowest levels in spots where the soil, though below high-water mark, is saturated by running or seeping fresh water. A series of quantitative determinations of the salinity of the soil-water in various of these habitats has been initiated, but determinations are not yet numerous or complete enough to allow of detailed discussion. The method being used is like that used by Harshberger (1909,

1912) in the study of the New Jersey marshes. It is hoped that the results of these determinations may be presented in a later paper by the junior author of this one.

5. THE TEMPERATURE OF THE WATER.

On the subject of the temperature of the water also we have no quantitative results to present. A few measurements of the temperature at the bottom and at the surface of the middle of the Inner Harbor at high tide (of 7.5 feet) were taken in July 1909, which showed a difference of but 1° or 1.5° C. In Miss Streeter's records made in July, the temperature of the stream at 600 south by 720 east was found to vary from 9° C. at low tide to 18° C. at high water. It is evident of course, that plants like *Zostera, Ruppia, Ulva,* etc., which lie on the black, heat-absorbing mud in the sun at low water, must often be heated to 30° or 35° C. or higher, in the summer. When, on the contrary, these plants are exposed at night, their temperature must fall at least to 10° C. or lower, since the air temperature may go down to 8° or lower during the growing season.

Just what part the seasonal change of water-temperatures plays directly, in determining the seasonal development of the algæ of the bottom, can not yet be stated. It is a well-known fact that the algal flora of a given locality varies markedly from winter to summer. In Section III of this paper it has been pointed out that not only are certain of the characteristic summer forms wanting in April and December, but in the former month, at least, *Ulva,* one species of *Ectocarpus,* and *Porphyra* were far more abundant in the Inlet than they have ever been in the summer. The rockweeds all about the harbor, which in summer bear practically no epiphytes, were found densely coated with filaments of *Ulothrix flacca.* In just how far the low temperatures of winter are directly responsible for the abundance of these algæ in winter, or whether they may be indirectly responsible by affecting the evaporation, has not yet been ascertained. Possibly, as Warming suggests (1909, p. 151), experimental physiological study may show that the larger proportion of dissolved O and CO_2 held by the water when cold offers the real explanation of the greater abundance of certain species in winter. The whole subject of the winter activities of marine plants is greatly in need of continuous study, such as has now become possible, with our many well-equipped marine laboratories.

V. SUMMARY AND CONCLUSIONS.

The Inner Harbor of Cold Spring Harbor has an area of 110 acres at high water. At low tide it has an area of 45 acres, with a maximum depth of 7 feet over an area only 100 feet in diameter. The mean range of tides is 7.75 feet.

By the aid of two series of perpendicular range-lines, marked with stakes, the positions of tide-lines, or of plants on the shore or in the harbor, could be accurately determined and recorded. A tide-curve was constructed from readings made on a tide-stake, and checked by one made later by a self-recording tide-gage. From this tide-curve the times of submergence and exposure of shore-levels, and thus of plants, were determined.

The chief vegetational zones or belts distinguished, with their upper and lower tidal limits, are the following: (1) The plankton, of Diatomaceæ and Peridineæ. (2) The bottom vegetation (-5 to $+1.5$ feet), including the "enhalid formation" of *Ulva, Enteromorpha, Zostera,* and *Ruppia;* the "lithophilous benthos" of *Enteromorpha, Ulva, Fucus, Pylaiella, Chondrus, Porphyra,* etc., attached to stones and shells, and the epiphytic algæ on *Zostera* and *Ulva,* chiefly diatoms, *Enteromorpha* and *Ceramium.* (3) The mid-littoral belt (1.5 to 6.5 feet). This is the most clearly limited belt about the harbor. It includes a *Spartina glabra* association on sloping shores and a rockweed association, of *Fucus, Ascophyllum,* and *Bostrychia,* on the wharves. (4) The upper littoral belt (6.5 to 8 feet), which has a more varied vegetation, including associations of felted filamentous algæ, of *Spartina patens,* of *Salicornia,* of *Suæda,* and of *Scirpus,* each either pure or mixed with members of one or more of the other associations mentioned, or with more or less scattered individuals of *Scirpus, Distichlis, Atriplex, Limonium,* or *Spergularia.* (5) The supra-littoral belt (8 to 12 feet). This is less clearly defined and more varied in make-up than the other belts. It includes associations composed of *Ammophila, Solidago, Salsola, Cakile,* and *Lathyrus,* of *Scirpus americanus* and *S. robustus,* of *Aspidium thelypteris,* and also includes more scattered and mixed groups of *Asclepias, Aster, Baccharis,* and *Hibiscus,* besides many upland plants.

The external environmental factors which influence the distribution of plants in this harbor are: substratum, water-currents, changes in water-level with the tides, salinity, and temperature of the water.

The substrata, aside from living plants, vary from fine silt, humus, or peat, to sand, gravel, rocks, and logs. The plant-covering at any level differs with the type of substratum, depending largely on the drainage possible. The soft, undrained mud of the very bottom of the harbor bears only *Zostera, Ruppia,* and anchored plants of *Ulva* and *Enteromorpha.* Other plants of the bottom, all of them algæ, require a firm substratum, as stone, a shell, or another plant, for attachment. The physical character of the soil greatly affects the rate of drainage of salt water from shore between the tide-lines and of fresh water from the upper levels, and thus determines the type of vegetation growing on them. For example, where the soil of the Spit above the 6-foot level is gravelly

and well-drained, *Spartina glabra* grows but little above this and is succeeded by *Salicornia* and *Suæda*, while on the peaty soil of flatter parts of the shore *S. glabra* may extend up to the 7.5-foot level and there be succeeded by *Spartina patens* or *Distichlis*. If fresh water is present in the fine soil of the upper levels, *Spartina glabra* is succeeded by *Scirpus americanus* and sometimes mingled with it up to the 8-foot level. On the Marsh the character of the vegetation of the surface is correlated with the local thickness of the peat above the underlying gravel.

The effects of water-currents on the distribution of plants are exercised by the dissemination of spores and seeds and by the breaking off and transportation of the shoots of *Zostera*, and of algæ like *Ulva, Enteromorpha, Fucus*, etc., which persist and grow in their new lodging-places. In other cases water-currents, by mechanically injuring the plants or by determining the character of the substratum, may favor or retard the further extension of a species. On the other hand, the rapid movement of the water is an evident advantage to some species, perhaps by increasing the interchange of material between the plant and the surrounding water, and possibly also by injuring competitors. Thus *Zostera, Cladophora, Pylaiella, Chondrus, Polysiphonia, Porphyra*, etc., are most abundant in or beside the rapid tidal current of the Inlet. *Ilea, Monostroma*, and *Pylaiella* likewise are abundant only in the rapidly flowing Creek entering the south end of the harbor.

A careful study of the vertical distribution of the littoral plants about this harbor shows that this depends primarily and very definitely on the relative time of their submergence and emergence with the rise and fall of the tide. Moreover, the vertical range of littoral species is strictly, sometimes very narrowly, limited. There are no species here, except two or three algæ, that are distributed "between tide-marks" (*i. e.*, from low water up to high water), as is so often reported. The nearest approach to this range found for any seed plant is that of *Spartina glabra*, whose vertical range of 5 feet (from 1.5 to 6.5 feet above mean low water) lies midway between the limits of the average (8-foot) tide. The range of this salt reed-grass covers but five-eighths of the mean tide-range and only half the range of many spring tides of the growing season (10 to 11 feet). This *Spartina* never gets below 1.5 feet and only in exceptionally moist and shaded areas does it grow at any appreciable distance above 6.5 feet. The alga *Fucus* ranges from just below mean low water up to 7.25 feet and *Enteromorpha intestinalis* has a similar range on shores where fresh-water rivulets flow in over the upper beach. The other seed plants of the shore range down to but 1.5 or 2 feet below mean high-water level (7.75 feet), with the exception of *Lilæopsis*, which is found between 5 and 6.5 feet. *Zostera* and *Ruppia* range upward for only 1 or 1.5 feet above mean low water.

The essential feature, for our purpose, of the tidal oscillation of water-level is the relative times of submergence and exposure experienced by the various shore-plants. For the sake of comparison this relation is most significantly expressed in a fraction for the upper limit and one for the lower limit of distribution of each species (p. 135). The influence of this change in water-level on the plant is effected through differences, at different levels, in evaporation rate; in aeration; in salinity of soil-water at higher levels; in exposure to rain and in light supply. It seems evident, for example, that *Spartina glabra*

and the rockweeds do not grow at levels above 6.5 feet, because they can not endure a greater evaporation than that experienced here. *Zostera* and many algæ for the same reason are confined to levels below mean low water, except where washed by tidal streams during low tide. It seems probable also that the too brilliant light or the exposure to rains during low tide prevents certain algæ from growing above mean low water. On the other hand, certain plants are stopped in their spread downward because they can not endure the longer submergence, with the lessened aeration and light supply, at lower levels. *Spartina glabra,* for example, as has been shown experimentally, is unable to persist more than a few months at levels even slightly below 1.5 feet. The rockweeds also seem unable to persist below the level just mentioned in the usually quiet and turbid water of the Inner Harbor. In the clearer, rapidly moving water of the Inlet, however, and especially in that of the Outer Harbor and Long Island Sound, *Fucus* grows a foot or more below mean low water.

The degree of salinity clearly determines the horizontal distribution of many plants in this harbor. For example, one series of algæ, chiefly Chlorophyceæ, occur only in the less saline south end of the harbor, where they are flooded with fresh water for from 2 to 10 hours each tide. On the other hand, the majority of the Florideæ found here grow in the channel to the Outer Harbor, where the water is most saline.

In the list of plants of the harbor (pp. 151 to 161), there are indicated for each species the physical characteristics of the habitat which are believed to be concerned with its distribution. In but relatively few instances has the connection between the distribution and external conditions been experimentally shown. Though the attempt has been made in the body of this paper to suggest the external factors determining the distribution of each common species, this must be regarded as a suggestion of the elements entering into the problem rather than as a statement of its definite solution.

It is believed that the determination of the relative time of submergence and exposure of a plant at its upper and its lower limit in this harbor, where the range of tide is about 8 feet, will make it possible to predict the vertical range of the same species in any other region, if the range of the tide is known. That is, the vertical range of a littoral plant is exactly proportional to the range of the tide.

In this study chief attention is devoted to determining and recording as accurately as possible the present distribution of the plants of this harbor in relation to tide-levels, salinity, and soils. Little has been said of the succession in time of the formations occurring at different levels on the shore. It is believed that this historical aspect of the problem can be solved more satisfactorily by the comparison of the vegetation that will exist here some years hence with that which is here recorded.

VI. LIST OF VASCULAR PLANTS OF THE BOTTOM AND SHORE, WITH VERTICAL RANGE AND THE PHYSICAL CHARACTERISTICS OF THE HABITAT OF EACH.

EXPLANATION OF TABLE F.

The data included in Table F are those listed immediately below, and they are indicated for each species found below the 12-foot level as far as known. Each characteristic of the plant or its environment is indicated in the proper column by a word or phrase, or, for the sake of brevity, by the symbol indicated in this list of data.

The 12 data noted for each species in Table F are arranged, in a horizontal line, in the following order:

I. Symbol: This is used to indicate the species on charts and plates.

II. Name of the species: The nomenclature in the case of ferns and seed plants is that of Gray's New Manual of Botany, seventh edition.

III. Habitat and persistence of the species:

1. Annual herb: an.
2. Biennial herb: bi.
3. Perennial herb: per.
4. Shrub or woody vine: sb.
5. Tree: tr.

IV. Density of stand or frequency of individuals of the species: A dash separating two symbols indicates that the density varies from the first to the second type.

1. Pure stand: pure. This is used only where a species may cover from several square decimeters to, in other cases (*e. g.*, of larger species), many square meters, with dozens, scores, or hundreds of individuals.
2. Mixed: preponderatingly, or nearly equally, with another species. This will be indicated by the use of the symbol for the second species thus: + Sp. means that the species in question has *Spartina patens* mixed with it.
3. Scattered: among a second species and less abundantly than it; *e. g.*, Sp. + indicates that the species is mingled with *Spartina patens* and is outnumbered by the latter.
4. Grouped or clumped: gpd.
5. Scattered, occasional, or isolated: oc.

V. Substratum: Of the 9 substrata listed the last 4 will be used only in the list of algæ.

1. Mud: md. This is soft, saturated soil, usually sparsely covered.
2. Humus: hu. Used for dry or moist humus-containing soils, except the peaty soil on the Marsh. It includes the very sandy humus of the top of the Spit.
3. Peat: pt. This includes soils, wet or moist, chiefly of organic origin, and bound together by dead and living roots and rhizomes.
4. Sand: sd. This may be dry, as at high levels on the Spit, or nearly saturated when between tide-marks.
5. Gravel: gv. Chiefly near high-water level.
6. Rock: rk. This includes larger pebbles, the stones of the wharves, and boulders of the bottom or shore.
7. Shells: sh. The shells of living and dead lamelli branch and gasteropods.
8. Wood: wd. Stakes, the logs of wharves, and sunken trunks or stakes on the bottom.
9. Living substratum: Chiefly *Mytilus edulis* among animals and *Zostera* and *Spartina glabra* among plants. Less commonly *Ulva* and the stouter red algæ may serve as substrata for certain diatoms and blue-green algæ. Thus, *e. g.*, ep./Z. means epiphytic on *Zostera*.

VI. Salinity of the soil water during the growing season: It may be more saline at levels above 8 feet in winter, due to storms, or, even in the growing season, the salinity may temporarily become somewhat greater near the high-water mark from the concentration due to evaporation. It may again be less saline at these upper levels after rains.

1. Salt: sa. By this is meant water of the density of that usually found at the surface of the harbor at high tide, which has a specific gravity of 1.019.
2. Brackish: br. Distinctly less dense than the above.
3. Fresh: fr.

VII. Light demands: That is, the light conditions under which the species usually grows.

1. Sun plants: su.
2. Shade plants: sd.

VIII. Upper limit of vertical distribution: The average upper limit of distribution of the species is given in feet above mean low water (indicated by the plus sign) or below mean low water (indicated by the minus sign). Where 12 feet + is used in this column it indicates that the plant may grow at this level, which is the highest level reached by winter tides, and at any level above this. That is, the plant is not confined to sea-coasts. In all other cases the upper limit given is the highest level at which the plant has been found about this harbor. Where but few individuals have been seen, and so the possible vertical range could not be determined with certainty, the one level at which it was found is indicated in this column and the column for the lower limit is left vacant.

IX. Lower limit of vertical distribution: The average recorded lower limit of distribution is given in feet, above or below mean low-water level for the soil upon which the plant grows at this limit. The extremes of distribution are given in Section III. The plus and minus signs are used as in column VIII to indicate levels above and below.

X. Emergence or exposure: This is given, in the average number of hours per lunar day, for the soil which bears the plants at the upper limit of the species. It thus indicates the greatest average exposure endured by any plants of the species, aside from the few exceptional individuals that may occur at slightly higher levels in habitats where the shade or moisture conditions are especially favorable. The data for emergence are taken from Table A (p. 135). Additional information concerning the occasional exposure of low levels and the duration of continuous exposure of higher levels may be obtained from Tables B and C (p. 136). The exposures during the hours of daylight may be seen from Table D, on page 142. Of course, the exposure of the soil on which a plant is growing indicates merely the exposure of the shoot above the soil. The subterranean portions are still immersed in a soil that may be practically saturated with salt water, *e. g.*, *Spartina glabra*, or with fresh water, *e. g.*, *Sagittaria latifolia*.

XI. Submergence: This is given for the soil on which the plant grows at the usual lower limit of distribution of the species, as indicated in column IX of Table F. The submergence given thus indicates in hours per lunar day of 24.9 hours, the average submergence endured by the lowest plants of the species in question during the growing season. The duration of submergence here given is taken from Table A (p. 135) and is calculated in the manner mentioned in the explanation of that table. The number of submergences per month or per growing season for plants near the high-water level, or the duration of continuous submergence of plants near mean low water, can be learned from Table B and Table C (p. 136). The occasional submergence of levels between 9 feet and 10 feet by storm tides is suggested in the cases of plants growing at these levels. Only winter storm tides ever cover levels much above 10 feet.

XII. Ratio of emergence to submergence: This is given for plants at the lower limit of vertical distribution of the species and at the upper limit. The two figures thus indicate the range in conditions, so far as the latter are affected by the tides, under which each species shows itself capable of growing here at Cold Spring Harbor. It is probable that if one had the tide-curve for a habitat with tides of greater magnitude like Nova Scotia or one with tides of lesser magnitude, like Virginia, he could predict the vertical range of any species common to one of these localities and to Cold Spring Harbor.

Table F.—*List of vascular plants, with analysis of the habitat of each.*

I. Symbol.	II. Name.	III. Habit.	IV. Density of growth.	V. Substratum.	VI. Salinity of soil water.	VII. Light demands.	VIII. Upper limit.	IX. Lower limit.	X. Average emergence endured per lunar day (24.9 hrs.) at upper limit.	XI. Average submergence endured per lunar day (24.9 hrs.) at lower limit.	XII. Ratio of emergence to submergence. At lower limit.	XII. At upper limit.
							Feet	*Feet*		*Hours*		
Av	Acalypha virginica L.	an	oc	pt	fr or br	su	12+	(?)	constant	(?)	(?)	∞
Ac	Acer rubrum L.	tr	oc	hu	fr	su	12+	8.50	constant	0.29	83.65	∞
Ae	Æthusa cynapium L.	an	oc	pt	fr or br	su	12+	....	constant	....	....	....
Ag	Agropyron repens (L.) Beauv.	per	oc to pure	sd & gv	br to fr	su	12+	8.25	constant	.57	42.76	∞
Ax	Agrostis sp.?	....	....	pt	br	su	....	....	constant	....	....	....
Ai	Ailanthus glandulosa Desf.	tr	oc	hu	fr	su	12+	9	constant	.07	353.09	∞
Al	Allium vineale. L.	per	oc	sd to hu	fr	su	12+	8.25	constant	.57	42.76	∞
Ak	Alnus incana (L.) Moench	sb	oc	hu	fr	su to sd	12+	9	constant	.07	353.09	∞
Am	Ambrosia artemisiæfolia L.	an	oc	sd to hu	fr to br	su	12+	8.25	constant	.57	42.76	∞
A	Ammophila arenaria (L.) Link	per	oc to pure	sd	fr to sa	su	12+	8.25	constant	.57	42.76	∞
An	Anaphalis margaritacea (L.) B. & H.	per	oc	sd to hu	fr to br ?	su	12+	8.75	constant	.16	157.51	∞
As	Asclepias incarnata L. pulchra Ehrb. (Pers.)	per	oc or Sa+	hu or pt	fr to br ?	su	12+	8.25	constant	.57	42.76	∞
Ao	Asparagus officinalis L.	per	oc	sd	fr	su	12+	9.50	constant	(1)	∞	....
At	Aspidium thelypteris (L.) Sw.	per	oc to pure	pt & hu	fr	su	12+	8.50	constant	.29	83.65	∞
Ab	Aster novæ-belgii L.	per	oc	pt	brk	su	12+	8.75	constant	.16	157.51	∞
Ar	Aster puniceus L.	per	oc	pt	brk	su	12+	....	constant	....	(?)	∞
Au	Aster subulatus Mich.	an	oc to gpd	pt	brk	su	9	7.25	24.81 hours	2	23.26	(?)
Af	Aster tenuifolius L.	per	oc	pt	brk	su	11	8	constant	1.02	23.26	∞
Aa	Atriplex arenaria Nutt.	an	oc to pure	sd or gv	brk to sa	su	8.50	6.50	24.6 hours	5.44	3.57	83.65
Ap	Atriplex patula L. hastata (L.) Gray	an	oc to pure	sd or pt	sa to br	su	8.50	6	24.6 hours	6.85	2.62	83.65
B	Baccharis halimifolia L.	sb	oc	hu to pt	brk to fr	su	9	7.50	24.81 hours	1.60	14.60	353.09
Ba	Barbarea stricta Andrz.	bi	oc	pt	fr to br	su	12+	8.75	constant	.16	157.51	∞
Bs	Benzoin æstivale (L.) Nees	sb	oc to gpd	hu	fr	su to sd	12+	8.50	constant	.29	83.65	∞
Bi	Bidens frondosa L.	an	gpd	hu or pt	fr	su	12+	....	constant	....	....	....
C	Cakile edentula (Bigel.) Hook	an	oc or gpd	sd	brk to sa	su	11±	8.50	constant	....	(?)	∞
Cb	Carex hormathodes Fernald	per	oc	pt	br or fr	....	....	....	....	....	....	....
Cd	Carex lurida Wahlenb.	per	oc	hu	fr	su	?	9	....	.07	353.09	∞
Ct	Carex straminea Willd.	....	....	....	....	....	....	....	....	....	....	....
Ce	Cerastium vulgatum L.	per	oc to gpd	sd or hu	fr to br	....	12+	....	constant	....	(?)	∞
Ca	Chenopodium album L.	an	oc or gpd	sd	br to sa	su	12+	8.50	constant	.29	83.65	∞
Cl	Chrysanthemum leucanthemum L.	per	oc	hu	fr	su	12+	9	constant	.07	353.09	∞
Cb	Cichorium intybus L.	per	oc	gr or hu	fr	su	12+	8.25	constant	.57	42.76	∞
Ci	Cicuta maculata L.	per	oc	hu	fr	su to sd	12+	8.25	constant	.57	42.76	∞
Cr	Clethra alnifolia L.	per	oc or gpd	hu	fr	su	12+	8.75	constant	.157	157.51	∞
Co	Convolvulus sepium L. pubescens (Gray) Fernald	per	oc or +Sd or +Sa	hu	fr	su to sd	12+	8.50	constant	.29	83.65	∞
Cu	Cuscuta gronovii Willd.	an	oc or gpd	Solidago	....	su	12+	8.75	constant	.157	157.51	∞
Cy	Cyperus filiculmis Vahl	per	oc or rare	sd or pt	br	su	12+	10.50	constant	(2)	∞±	∞
Da	Dactylis glomerata L.	per	oc	pt	br to fr	su	12+	9	constant	.07	353.09	∞
Du	Daucus carota L.	bi	oc	hu	fr	su	12+	9	constant	.07	353.09	∞

[1] By storm tides.

[2] Winter storm tides.

TABLE F.—*List of vascular plants, with analysis of the habitat of each*—Continued.

I. Symbol.	II. Name.	III. Habit.	IV. Density of growth.	V. Substratum.	VI. Salinity of soil water.	VII. Light demands.	VIII. Upper limit.	IX. Lower limit.	X. Average emergence endured per lunar day (24.9 hrs.) at upper limit.	XI. Average submergence endured per lunar day (24.9 hrs.) at lower limit.	XII. Ratio of emergence to submergence. At lower limit.	At upper limit.
							Feet	*Feet*		*Hours*		
Di	Dianthus armeria L.	an.	oc.	hu	fr.	su.	12+	....	constant.	....	....	∞
D	Distichlis spicata (L.) Greene	per.	oc+Sp.pure Sp+	sd to pt.	br to sa.	su.	8.25	6.50	24.31 hours.	5.44	3.57	42.76
El	Eleocharis olivacea Torr.	per.	oc or Sp+	pt.	br to fr.	su.	12+	8.50	constant.	.29	88.65	∞
Ed	Epilobium coloratum Muhl	per.	oc.	pt.	fr to br.	su.	12+	9	constant.	.07	358.09	∞
Eq	Equisetum arvense L.	per.	gpd.	hu	fr.	su.	12+	9	constant.	.07	358.09	∞
Eg	Eragrostis minor Host	an.	oc.	sd to hu.	fr.	su.	12+	9	constant.	.07	358.09	∞
E	Erechtites hieracifolia (L.) Raf.	an.	oc.	pt or hu.	fr.	su.	12+	9	constant.	.07	358.09	∞
Ea	Erigeron annuus (L.) Pers.	an.	oc.	hu	fr.	su.	12+	8.50	constant.	.29	88.65	∞
Ec	Erigeron canadensis L.	an.	oc.	hu	....	su.	12+	8.75	constant.	.16	157.51	∞
Et	Eupatorium perfoliatum L.	per.	oc.	hu	fr.	su.	12+	8.25	constant.	.57	42.76	∞
Ep	Eupatorium purpureum L.	per.	oc.	hu	fr.	su.	12+	8.25	constant.	.57	42.76	∞
Em	Euphorbia maculata L.	an.	oc.	sd to hu.	fr ?	su.	12+	9	constant.	.07	358.09	∞
Eu	Euphorbia polygonifolia L.	as.	oc.	sd.	br to fr.	su.	12+	8.50	constant.	.29	88.65	∞
Fr	Fragaria virginiana Duchesne	per.	oc.	hu	fr.	su.	12+	....	constant.	....	....	∞
F	Fraxinus americana L.	tr.	oc.	hu	fr.	su.	12+	9	constant.	.07	358.09	∞
Ga	Galium claytoni Mich.	per.	oc+C & Sd.	sd to hu.	sa to br.	su.	12+	8	constant.	1.02	23.26	∞
G	Gerardia maritima Raf.	an.	oc gpd or Sp+	pt.	br.	su to sd.	8.75	8	24.72 hours.	1.02	23.26	157.51
Gd	Gleditsia triacanthos L.	tr, sb.	oc.	sd to hu.	fr. ?	su.	12+	9.50	constant.	([3])	∞±	∞
Gn	Gnaphalium (polycephalum ?)	per.	oc.	sd to hu.	fr.	su.	12+	9	constant.	.07	358.09	∞
H	Hibiscus moscheutos L.	per.	oc or gpd	pt or hu.	br to fr.	su.	12±	8	constant.	1.02	23.26	∞
Hc	Hypericum canadense L.	an ?	oc.	hu	fr.	su.	12+	(?)	constant.	(?)	....	∞
Hm	Hypericum mutilum L.	an ?	oc.	hu	fr.	su.	12+	(?)	constant.	(?)	....	∞
Hp	Hypericum perforatum L.	per.	oc or ?	hu	fr.	....	12+	(?)	constant.	(?)	....	∞
Hv	Hypericum virginicum L.	per.	oc – gpd.	hu or pt.	fr, br.	su.	12+	9.00	constant.	.07	358.09	∞
Ib	Impatiens biflora Walt.	an.	oc or gpd.	hu	fr.	sd.	12+	9	constant.	.07	358.09	∞
I	Iris versicolor L.	per.	gpd.	hu	fr.	su to sd.	12+	7.25	24.31 hours.	2	11.45	42.76
Iv	Iva oraria Bartlett	per.	oc & gpd	pt or hu.	br to fr.	su.	8.50	7.50	24.59 hours.	1.60	14.60	88.65
Jc	Juncus canadensis J. Gay	per.	oc.	hu	fr.	su.	12+	8.50	constant.	.29	88.65	∞
J	Juncus Gerardi Loisel	per.	pure, +Sp, Sp+.	pt.	sa to br.	su.	8.25	7.25	24.31 hours.	2	11.45	42.76
Jt	Juncus tenuis Willd.	per.	oc.	pt to hu.	fr.	su.	12+	9	constant.	.07	358.09	∞
Jv	Juniperus virginiana L.	tr.	oc.	hu	fr.	su.	12+	9	constant.	.07	358.09	∞
Lc	Lactuca (canadensis ?)	bi.	oc.	sd to hu.	fr to ?	su.	12+	....	constant.	....	....	∞
Lm	Lathyrus maritimus (L.) Bigel.	per.	oc – gpd.	sd.	br to fr.	su.	12 ?	11	constant.	0	∞	....
Le	Leersia oryzoides (L.) Sw.	per.	oc.	pt ?	br to fr.	su to sd.	....	....	....	....	....	....
Li	Lilæopsis lineata (Mich.) Greene	per.	gpd – pure	md & gv.	fr to sa.	su to sd.	6.50	5.50	19.44 hours.	7.85±	2.17	3.57
L	Limonium carolinianum (Walt.) Britton	per.	oc, gpd, pure.	sd to pt.	sa to br.	su.	8.25	7.25	24.31 hours.	2.00±	11.45	42.76
La	Lycopus americanus Muhl.	per.	oc.	hu	fr.	su to sd.	12+	9.25	constant.	([3])	∞	....

[3] By storm tides.

TABLE F.—*List of vascular plants, with analysis of the habitat of each*—Continued.

I. Symbol.	II. Name.	III. Habit.	IV. Density of growth.	V. Substratum.	VI. Salinity of soil water.	VII. Light demands.	VIII. Upper limit.	IX. Lower limit.	X. Average emergence endured per lunar day (24.9 hrs.) at upper limit.	XI. Average submergence endured per lunar day (24.9 hrs.) at lower limit.	XII. Ratio of emergence to submergence. At lower limit.	XII. Ratio of emergence to submergence. At upper limit.
							Feet	*Feet*		*Hours*		
Lv	Lycopus virginicus L.	per.	oc.	hu	fr	su.	12+	9	constant.	.07	358.09	∞
Ly	Lysimachia terrestris (L.) B. S. P.	per.	oc.	hu	fr	su.	12+	8	constant.	1.02	23.26	∞
Me	Melilotus alba Desr.	an	oc to gpd.	hu to gv.	fr.	su to sd.	12+	8.75	constant.	.16	157.51	∞
Ml	Mollugo verticillata L.	an	oc	sd to hu.	fr.	su.	12+	9.00	constant.	.07	358.09	∞
Mc	Myrica (cerifera ?).	sb.	oc	hu to pt.		su.	12+	8.75	constant.	.16	157.51	∞
M	Myrica Gale L.	sb.	oc	pt or hu.	fr to br ?	su.	12+	9	constant.	.07	358.09	∞
Np	Nepeta cataria L.	per.	oc + Co.	sd to hu.	fr to br.	su.	12+	11.50	constant.	(5)	∞	∞
O	Oenothera biennis ;	bi.	oc to gpd.	sd to hu.	fr to br ?	su.	12+	11	constant.	(5)	∞	∞
On	Onoclea sensibilis L.	per.	oc & gpd.	hu or pt.	fr.	su.	12+	9	constant.	.07	358.09	∞
Ox	Oxalis stricta L.	per.	oc.	sd to hu.	fr.	su.	12+	9	constant.	.07	358.09	∞
Pa	Panicum sp. ?	per.	oc.	hu	fr to br.	su.	12+	8	constant.	1.02	23.26	∞
Pe	Periploca græca L.	sb.	1 example.	hu	fr to br ?	su.	12+	9	constant.	.07	358.09	∞
Ph	Phleum pratense	per.	(?)			su.	12+		constant.			∞
Pd	Plantago decipiens Barneoud	per.	oc to gpd.	md or pt.	sa to br.	su.	8.25	6.25	24.81 hours.	6.88	3.16	42.76
Pl	Plantago lanceolata L.	per.	oc.	hu	br to fr.	su.	12+	9	constant.	.07	358.09	∞
Pm	Plantago major L.	per.	oc.	hu or pt.	fr to br.	su.	12+	6.25	constant.	.57	42.76	∞
Pc	Pluchea camphorata (L.) D. C.	an	gpd	pt.	br.	su.		8.25		.57	42.76	
P	Poa compressa L.	per.	pure, A+	sd.	fr.	su.	12+	10.75	constant.	(4)	∞	
Pp	Poa pratensis L.	per.	gpd.	sd to hu.	fr to br.	su.	12+	8.25	constant.	.57	42.76	∞
Pb	Polygonella articulata (L.) Meisn.	an	oc.	sd to hu.	fr.	su.	12+	10	constant.	(5)	∞	
Pi	Polygonum lapathifolium L.	an	oc.	hu	fr.	sd.	12+	9	constant.	.07	358.09	∞
Pr	Polygonum maritimum L.	per.	oc.	md.	sa.	su.	(?)	6		6.85	2.62	(?)
Pg	Polygonum pennsylvanicum L.	an	oc.	hu	fr.	su to sd.	12+	(?)	constant.			
Ps	Polygonum sagittatum L.	an	oc.	hu	fr.	sd to su.	12+	9		.07	358.09	∞
Px	Polygonum scandens L.	per.	oc.	sd to hu.	fr to br.	su.	12+	9	constant.	.07	358.09	∞
Pu	Portulaca oleracea L.	an	oc.	sd to hu.	fr.	su.	12+	10	constant.	(3)	∞	∞
Po	Potentilla argentea L.	per.	oc.	hu to gv.	fr.	su.	12+		constant.	?		∞
Pv	Prunus avium L.	tr.	oc.	hu	fr.	su.	12+	9	constant.	.07	358.09	∞
Pn	Prunus serotina Ehrb.	tr.	oc.	hu	fr.	su.	12+	9	constant.	.07	358.09	∞
Pq	Psedera quinquefolia (L.) Greene	sb.	oc.	hu to sd.	fr to br.	sd to su.	12+	9	constant.	.07	358.09	∞
Pt	Ptilimnium capillaceum (Mich.) Raf.	an	oc.	pt.	br to fr ?	su to sd.		?		?		
Py	Pyrus malus L.	tr.	oc.	hu	fr.	su.	12+	8.75	constant.	.16	157.51	∞
Q	Quercus sp. ?	seed 1.		sd.	fr.	su.	12+	11	constant.	(3)	∞	∞
Rg	Rhus glabra L.	sb.	gpd and oc.	sd & hu.	fr.	su.	12+	11	constant.	(3)	∞	∞
R	Rhus toxicodendron L.	sb.	gpd and oc.	hu & sd.	fr.	su.	12+	9	constant.	.07	358.09	∞
Rv	Rhus vernix L.	sb.	oc.	hu	fr.	sd.	12+	9	constant.	.07	358.09	∞
Ro	Robinia Pseudo Acacia L.	tr.	oc.	hu to sd.	fr.	su.	12+	9	constant.	.07	358.09	∞
Rs	Rosa carolina L.	sb.	oc to gpd.	hu	fr.	su.	12+	8.75	constant.	.16	157.51	∞

[3] Winter storm tides. [5] Storm tides.

TABLE F.—*List of vascular plants, with analysis of the habitat of each*—Continued.

I. Symbol.	II. Name.	III. Habit.	IV. Density of growth.	V. Substratum.	VI. Salinity of soil water.	VII. Light demands.	VIII. Upper limit.	IX. Lower limit.	X. Average emergence endured per lunar day (24.9 hrs.) at upper limit.	XI. Average submergence endured per lunar day (24.9 hrs.) at lower limit.	XII. Ratio of emergence to submergence. At lower limit.	XII. At upper limit.
							Feet	*Feet*		*Hours*		
Rb	Rubus alleghaniensis Porter	sb.	oc.	hu	fr.	su.	12+	9	constant	.07	353.09	∞
Ra	Rumex acetosella L.	per.	gpd to oc.	hu	fr.	su.	12+	8.25	constant	.57	42.76	∞
Rc	Rumex crispus L.	per.	oc or gpd	hu	fr to br?	su.	12+	8.50	constant	.29	83.65	∞
Ru	Ruppia maritima L.	per ?.	gpd.	md.	sa.	su.	+1	0	6.09 hours	23.06	.079	.324
Sg	Sagittaria latifolia Willd.	per.	oc.	hu	fr.	su.	12+	9	constant	.07	353.08	∞
Sm	Salicornia ambigua Mich.	per.	oc or gpd.	gv or pt.	sa to br.	su.	7.50	6	23.28 hours	6.85	2.62	14.60
Se	Salicornia europæa L.	an.	pure, +Su, or oc.	gv to pt.	sa to br.	su.	7.50	6.50	23.28 hours	5.44	3.57	14.60
Sx	Salix sp. ?	tr.	oc.	sd to hu.	fr.	su.	12+	11.75	constant	([4])	∞	....
Sk	Salsola kali L.	an.	oc.	sd	sa to br.	su.	12+	8.50	constant	.29	83.65	∞
Sb	Sambucus canadensis L.	sb.	oc or gpd.	hu	fr.	su to sd.	12+	8.50	constant	.29	83.65	∞
Sl	Samolus floribundus H. B. K.	per.	oc.	hu	fr.	su.	12+	7.50	constant	1.60	14.60	∞
Sa	Scirpus americanus Pers.	per.	pure, +Sp, +S.	pt or md	br to fr.	su.	12+	6.50	constant	5.44	3.57	∞
Sn	Scirpus nanus Spreng.	per.	pure to oc.	md.	sa to br.	su to sd.	8	6	23.86 hours	6.85	2.62	23.26
Sr	Scirpus robustus Pursh.	per.	+S+Sa or pure.	pt to hu.	br to fr.	su.	8.50	7	24.59 hours	2.67	6.59	83.65
Se	Selaginella apus (L) Spring.	per.	oc.	hu	fr to br.	su to sd.	12+	9	constant	.07	353.09	∞
St	Setaria viridis (L) Beauv.	an.	oc to gpd.	sd to hu.	fr to br.	su.	12+	9	constant	.07	353.09	∞
So	Solanum dulcamara L.	per.	oc.	hu	fr.	su to sd.	12+	8.25	constant	.57	42.76	∞
Sa	Solidago canadensis L.	per.	oc or gpd.	hu	fr.	su.	12+	8.50	constant	.29	83.65	∞
Sd	Solidago sempervirens L.	per.	oc or gpd.	sd hu pt.	sa to fr.	su.	12+	6.50	constant	5.44	3.57	∞
Sc	Sonchus asper (L) Hill	an.	oc.	pt.	br	su to sd.	12+	8	constant	1.02	23.26	∞
S	Spartina glabra Muhl. var. alterniflora (Loisel) Merr.	per.	pure or gpd.	md to pt.	sa to fr.	su to sd.	6.50	1.50	19.44 hours	16.79	.481	3.57
Sp	Spartina patens (Ait.) Muhl.	per.	pure+D+J.	sd md pt	sa to br.	su.	8.25	6.50	24.31 hours	5.44	3.57	42.76
Sl	Spergularia marina (L.) Griseb.	an.	gpd or pure.	sd gv md	br.	su.	8	7	23.86 hours	2.67	6.59	23.26
Su	Suæda maritima (L.) Dumort.	an.	pure+Se oc.	sd to pt.	sa to br.	su.	8	6.50	23.86 hours	5.44	3.57	23.26
Sy	Symplocarpus fœtidus (L.) Nutt.	per.	oc to gpd.	hu	fr.	sd.	12+	9	constant	.07	353.09	∞
Tx	Taraxacum officinale Weber	per.	oc.	hu	fr to br?	su.	12+	9	constant	.07	353.09	∞
Te	Tecoma radicans (L.) Juss.	sb.	oc.	sd to hu.	fr.	su.	12+	11	constant	([4])	∞	∞
Ti	Tilia americana L.	tr.	oc.	hu	fr.	su.	12+	9	constant	.07	353.09	∞
Ta	Trifolium agrarium L.	per.	oc.	hu	fr.	su.	12+	10	constant	([5])	∞	∞
Tp	Trifolium pratense L.	per.	oc.	hu	fr.	su.	12+	8.25	constant	.57	42.76	∞
T	Triglochin maritima L.	per.	oc.	md.	sa to br?	su.	7.50	6.25	23.28 hours	6.88	3.16	14.60
Ty	Typha angustifolia L.	per.	oc to gpd	hu, pt.	fr to br.	su.	12+	....	constant	....	....	....
Va	Vaccinium pennsylvanicum Lam.	per.	oc.	hu.	fr to br.	su.	....	9	....	.07	353.09	∞
Ve	Verbascum thapsus L.	bi.	oc or gpd.	sd to hu.	fr.	su.	12+	9	constant	.07	353.09	∞
Vn	Vernonia sp. ?	per.	oc.	hu	fr.	su.	12+	8.50	constant	.29	83.65	∞
Vi	Vitis labrusca L. (Concord)	sb.	1 example.	hu	fr.	su.	12+	8.75	constant	.16	157.51	∞
Xn	Xanthium echinatum Murr.	an.	oc or gpd.	sd, hu.	fr to br.	su.	11.50	8	constant	1.02	23.26	∞
Z	Zostera marina L.	per.	pure to gpd oc.	md.	sa.	su to sp.	1	−3	6.09	Constant.	0	.324

[4] Winter storm tides. [5] Storm tides.

VII. LIST OF THALLOPHYTES OCCURRING BELOW THE 10-FOOT LEVEL.

EXPLANATION OF TABLE G.

In addition to the algæ, 2 bacteria, 2 lichens, and 2 bryophytes have been recorded. All of these are given at the end of this list of algæ. The names used for green algæ are those of F. S. Collins (Chlorophyceæ of North America). Those used for the Phæophyceæ and Rhodophyceæ are chiefly from Farlow's "Marine Algæ of New England."

While the number of lower plants growing on the east and west shores, between the 9-foot and 12-foot levels, may be considerable, they are, as far as noted, such as occur far above sea-level. Therefore, aside from the algæ of the fresh-water rivulets, they are not here listed. The lichens and mosses of the Spit, even from the top, are included, because this is such an essentially littoral habitat.

Symbols are given for part of the forms only in this table, these being the ones whose distribution is indicated by means of these symbols on plates IX and X. In cases where the distribution was not determined separately for each of the several species of a genus, the same symbol has been used on the maps to indicate any species of the genus found in a given locality. This collective use of a symbol is indicated in Table G by a bracket embracing the various species included under it.

The characters of the plants and their environments which are noted in Table G are those given for the vascular plants, with the exception of "light demands." These are omitted because few definite and significant data are available. Of course, many of the algæ of the bottom and wharves, growing between tide-marks, are in a sense shade plants, protected by submergence, as was suggested in regard to *Zostera* and *Ruppia* in Section V. Other algæ growing between the 4-foot and 7-foot levels among the stalks of *Spartina glabra, S. patens,* and the *Salicornias* are also shaded by these larger plants. Other species still, like those of *Calothrix* and *Lyngbya,* grow in full sunlight on the open beach, or on the wharves even near the 8-foot level. These are subjected to rather intense light and desiccation, and during neap tides may not be touched by the water for several days together. Finally, the algæ of the Inlet below —1.5 feet and those of fresh-water streams are never exposed to full sunlight.

Certain algæ, *e. g., Ulva, Agardhiella, Fucus vesiculosus spiralis,* etc., may persist for weeks or months unattached to the substratum. Where a species may occur free in this manner this fact is indicated in the column for substratum by the symbol "fr."

Since none of the algæ penetrate far into the substratum, the salinity of the soil-water is of little consequence to them. The salinity of water surrounding the shoot is the thing of importance, and it is this, therefore, that is given in the list. This salinity may, as is indicated, differ greatly at different stages of the tide. This is especially true for plants living near fresh-water streams. But

TABLE G.—*List of thallophytes, with the habitat of each species.*

I. Symbol.	II. Name.	III. Habit or persistence.	IV. Density of growth.	V. Substratum.	VI. Salinity of submerging water.	VII. Upper limit.	VIII. Lower limit.	IX. Average emergence endured per lunar day (24.9 hrs.) at upper limit.	X. Average submergence endured per lunar day (24.9 hrs.) at lower limit.	XI. Ratio of emergence to submergence during growing season. At lower limit.	XI. At upper limit.
						Feet.	*Feet.*	*Hours.*			
At	Agardhiella tenera (J. Ag.) Schmitz	per ?	oc to abund, often fr.	rk, peb, sh	sa	+1	−1.50	6.09	constant	0	.324
	Amphithrix zanthina		oc	rk	fr to sa	+7.50	+6	23.28	6.85 hours.	2.62	14.60
Ab	Anabæna torulosa (Carmich. Lagh.)	an	pure to oc	md, wd	sa to br.	7	4	21.27	11.45 hours.	1.17	6.59
	Anabæna variabilis		oc	md, pt	sa to br.	7		21.27			6.59
A	Ascophyllum nodosum Le Jolis	per	pure, + Fv, oc.	rk, wd, sh	sa to fr.	7	−1		24.76 hours.	.005	6.59
Bo	Bostrychia rivularis Harvey	per	pure, + Fv, oc.	rk, wd, Fv, A	sa	7	+3	21.27	18.81 hours.	.852	6.59
Br	Bryopsis plumosa (Huds.) Agardh		oc	rk	sa	4		13.43			1.17
	Callithamnion roseum (Roth.) Harvey		oc	peb	sa	1		6.09			.324
	Calothrix crustacea (Bornet and Thuret)	per	pure to oc	rk, wd	sa	8	6	23.86	6.85 hours.	2.62	23.26
	Calothrix crustacea prolifera		oc to pure	wd	sa	8	6?	23.86	6.85 hours.	3.57	23.26
Cx	Calothrix fuscoviolacea	per	pure to oc	rk, wd	sa	7.50	6.5	23.28	5.44 hours.		14.60
	Calothrix pulvinata Agardh	per	pure to oc	sd	sa	7.50	(?)	23.28		2.62	14.60
	Calothrix scopulorum Agardh	per ?	pure to oc	grav	sa	7	6	21.27	6.85 hours.	0	6.590
Cr	Ceramium rubrum Agardh	an ?	oc to gpd	rk, ep/Z	sa	1.50	−2	8.08	constant	0	.480
Cs	Ceramium strictum Harvey	an ?	oc, gpd, + Cr	ep/Z	sa	1.50	−2	8.08	constant	0	.480
Ct	Chætomorpha æra (Dilw.) Kütz forma linum (Fl. Dan.)		oc, + R, + Cl.	md	sa	±0		1.82			.079
	Chætomorpha sp. ? (cells 100 mu. diam.)		oc	ep/S	sa	6.5	+4	19.45	11.45 hours.	1.17	3.574
	Chamæsiphon sp ?		oc	ep/Cl.	sa to fr.	2.5		9.90			.666
	Chondria tenuissima Ag		oc, fr.	rk	sa	− .5	−2	0.79	constant	0	.0815
Ch	Chondrus crispus (L.) Stack	per	oc to gpd	rk	sa	0	−2	1.82	constant	0	.079
	Chroococcus turgidus Naeg	an ?	oc	ep/S	sa	6.50		19.44			35.74
Cl	Cladophora (expansa ?) (Mert.) Kütz	(?)	oc, + Rz, + Lg, pure.	md, gv	sa to br.	7.25	2	22.90	15.95 hours.	.55	11.45
	Cocconeis scutellum Ehrb	per	oc	ep/Z, ep/U, etc.	sa to br.	1	−2	6.09	constant	0	.324
Da	Dasya elegans Ag	(?)	oc	rk	sa	0	−3	1.82	constant	0	.079
Dl	Delesseria leprieurii Mont	(?)	oc to pure	rk, wd	sa	5	+1	15.59	18.78 hours.	.324	1.074
Ea	Ectocarpus siliculosus amphibius. Harv	an ?	oc to pure	rk	fr to sa	1	1	6.09	18.78 hours.	.324	.324
Ep	Ectocarpus confervoides penniciliformis Le Jolis	an ?	oc	rk	sa	0		1.82			.079
	Ectocarpus (sp. ?)	(?)	oc	rk	sa	6	5	18.08	9.29 hours.	1.674	2.625
Ec	Enteromorpha clathrata Roth. Grev	per	oc, gpd, pure	rk, wd, ep/Z	sa	7	−1	21.27	24.76 hours.	.005	6.593
	Enteromorpha crinita (Roth.) J. G. Ag	per	oc to pure	pt	br to sa.	5.50		16.80±			2.08
Ei	Enteromorpha intestinalis (L.) Grev	per	oc to pure	rk, wd	fr to sa.	7.25	0	22.90	23.06 hours.	.0788	11.45
	Enteromorpha minima Naeg. in Kütz	(?)	oc	rk	sa	7		21.27			6.593
	Enteromorpha prolifera (Fl. Dan) J. G. Ag	per ?	oc to pure	rk	sa to fr.	6	5	18.08	9.29 hours.	1.674	2.625

TABLE G.—*List of thallophytes, with the habitat of each species.*—Continued.

I. Symbol.	II. Name.	III. Habit or persistence.	IV. Density of growth.	V. Substratum.	VI. Salinity of submerging water.	VII. Upper limit.	VIII. Lower limit.	IX. Average emergence endured per lunar day (24.9 hrs.) at upper limit.	X. Average submergence endured per lunar day (24.9 hrs.) at lower limit.	XI. Ratio of emergence to submergence during growing season. At lower limit.	XI. At upper limit.
						Feet.	*Feet.*	*Hours.*			
Fe	Fucus evanescens Ag.	per	oc, + Fv, + As	rk, wd	sa to br.	7.25	5	22.90	9.29 hours.	1.674	11.45
Fv	Fucus vesiculosus L.	per	oc, + Bo, + Fe, + As, pure.	rk, sh, wd	sa to br.	7.25	0	22.90	23.06 hours.	.079	11.45
Fs	Fucus vesiculosus spiralis Auct.	per	oc to pure	rk, sh or fr	sa	6	1.50	18.08	16.80 hours.	.481	2.625
Gc	Gracilaria multipartita Ag.	per	oc	rk, sh	sa	1	−2	6.09	constant	0	.324
Gn	Grinnellia americana Harv.	(?)	oc	rk, sh	sa	1	−3	6.09	constant	0	.324
H	Hildenbrandia prototypus Nardo	per	oc or common	rk	sa to fr.	7	−1 ?	21.27	24.76 hours.	.005	6.598
Il	Ilea fulvescens (Ag.) J. G. Ag.	per?	pure to oc	rk	fr, br, sa	7	+1.50	21.27	16.80 hours.	.481	6.598
	Isactis plana Thuret	(?)	oc	pt	br to sa.	6		18.08			2.625
	Lomentaria uncinata Menegh.	(?)	oc	rk	sa	−1.50		0			0.0
Lg	Lyngbya aestuarii Liebm.	per	pure, + Mi, + V, oc.	pt, md, ep/S	br to sa.	7	4	21.27	11.45 hours.	1.172	6.598
Ll	Lyngbya lutea	per?	oc to pure	wd, pt, rk	sa	7	2	21.27	15.95 hours.	.55	6.598
Ls	Lyngbya semiplena	per?	oc, + Rz, Rz +, etc.	pt, gv, sd	br to sa.	7.50	6.50	23.28	5.44 hours.	3.574	14.60
	Lyngbya (sp. 1 to 5)	(?)	oc, Lg +, Rs +	rk, wd, pt, md	sa to br.	7	4	21.27	11.45 hours.	1.172	6.598
Mb	Melosira borrei Grev.	per?	oc, grpd	ep/Z, wd, etc.	sa or br.	1.50+		8.08			.481
Mn	Melosira nummuloides (Bory) Ag.	per	oc, grpd	pt, ep/Z, ep/U, ep/Ey, ep/Bo	sa or br.	6.50	−1	19.44	24.76 hours.	.005	3.574
Mi	Microcoleus chthonoplastes Thuret	per	pure, + Lg, Rz +, Ec +	md, trash	sa or br.	7.50	+4	23.28	11.45 hours.	1.172	14.60
	Microcoleus tenerrimus	(?)	oc, Mi +	md, flood trash	sa or br.	6.50		19.44			3.574
	Microspora [amœna (Kütz) Rabenhorst ?]	(?)	oc	rk, md, pt	sa or br.	7.50	6	23.28	6.85 hours.	2.625	14.60
M	Monostroma latissimum (Kütz) Wittr.	per?	oc, grpd to pure	rk, wd, ep/S	fr to sa.	7.50	2.50	23.28	14.90 hours.	.666	14.60
	Monostroma (crepidinum Farlow. ?)	(?)	oc	rk	fr to sa.	5		15.59			1.674
	Myrionema vulgare Thuret	(?)	oc	rk	sa	5		15.59			1.674
N	Navicula grevillei (Ag.) Cleve	per	oc to grpd	ep/Z, md, wd	sa	1	−1	6.09	24.76 hours.	.005	.324
	Navicula (kennedyi W. S. ?)	per?	oc	wd	sa	0		1.82			.079
	Nostoc (sp. ?)	(?)	oc	md	fr to sa.	7.50	+7	23.28	2.67 hours.	6.598	14.60
	Oscillatoria limosa Kütz.	(?)	oc	md	sa	6.50	6	19.44	6.85 hours.	2.625	3.574
	Oscillatoria (sp. 1 to 6)	(?)	oc, grpd, + Lg.	md, cp/S, iron pump.	sa to fr.	6.50	0	19.44	23.06 hours.	.079	3.574

TABLE G.—*List of thallophytes, with the habitat of each species.*—Continued.

I. Symbol.	II. Name.	III. Habit or persistence.	IV. Density of growth.	V. Substratum.	VI. Salinity of submerging water.	VII. Upper limit.	VIII. Lower limit.	IX. Average emergence endured per lunar day (24.9 hrs.) at upper limit.	X. Average submergence endured per lunar day (24.9 hrs.) at lower limit.	XI. Ratio of emergence to submergence during growing season. At lower limit.	XI. At upper limit.
						Feet.	*Feet.*	*Hours.*			
	Petrocelis cruenta Ag.	(?)	oc	rk	sa to br.	4	2	13.43	15.95 hours.	.55	1.172
	Pleurosigma angulatum W. S.	per ?	oc, (felts of algæ)	gv md	sa	6.25		18.55			3.161
	Pleurosigma intermedium W. S.	(?)	oc	gv md	sa	0		1.83			.079
	Polycystis elabens Kütz.	(?)	oc	md	sa	7		21.27	constant		6.598
Pv	Polysiphonia variegata Ag.	an ?	oc	rk	sa	0	−2.50	1.83		0	.079
Pr	Porphyra laciniata Ag.	per ?	oc to pure	rk, wd	sa	4	0	13.43	23.06 hours.	.079	1.172
Py	Pylaiella littoralis Kjellm.	(?)	oc to tufted	rk, wd	sa to fr.	4.50	−1.50	14.45	constant	0	1.385
Rf	Ralfsia clavata Crouan	an ?	oc to pure	wd, rk	sa	5	(?)	15.59			1.674
	Rhizoclonium riparium Roth	per ?	oc, Rs+, etc.	md, sd	sa	7.50	+6	23.23	6.85 hours.	2.625	14.60
R	Rhizoclonium tortuosum Kütz.	per	pure, +V, +Lg, +Cl, +Ec, or oc	rk, ep/S, wd, md.	sa to br.	8	2	23.86	15.95 hours.	.55	23.259
Rv	Rivularia atra Roth	an ?	gpd to colonies	md	sa to br.	6	5	18.03	9.29 hours.	1.674	2.625
	Rivularia plicata Carm.	(?)	oc, Rs+	md	sa to br.	7.50	?	23.23			14.60
S	Scytosiphon lomentarius Ag.	(?)	oc, gpd to pure	rk	sa	1	−1.50	6.095	constant	0	.324
Sp	Spirulina tenuissima Kütz.	(?)	pure to oc	ep/Z, ep/U, md.	sa	7	0	21.27	23.06 hours.	.079	6.598
	Synedra affinis Kütz.	(?)	oc	ep/algæ	sa	4	0	13.43	23.06 hours.	.079	1.172
Ux	Ulothrix flacca (Dillw.) Thuret	an ?	oc to pure	ep/Fv, ep/As, wd	sa	6.50	3	19.44	13.81 hours.	.852	3.574
	Ulothrix implexa Kütz.	(?)	oc	rk	fr to sa.	7.25	6	22.90	6.85 hours.	2.62	11.45
U	Ulva lactuca L. var. latissima (L.) D. C.	per	pure to oc	rk, wd or fr	sa to br-fr	4	−5	13.43	constant	0	1.172
V	Vaucheria Thuretii Wor ?	per ?	pure, Lg+, Rs+	md, pt	sa to fr.	7	5	21.27	9.29 hours.	1.674	6.598
	SCHIZOMYCETES.										
	Beggiatoa mirabilis	(?)	frequent	in md	sa to br.	5	1	15.59	18.78 hours.	.324	1.674
	Lamprocystis roseo-persicina Winogradski	per ?	pure to oc	md, fr	sa to br.	7.25		22.90			11.45
	LICHENES.										
	Cladonia sp. ?	per	oc	sd to hu	fr to sa.	12+	9	constant	.07 hour.	353.09	∞
	Lecanora subfusca (L.) Ach.	per	oc	wd	fr to sa.	12+	8	constant	1.02 hours.	23.26	∞
	BRYOPHYTES.										
	Two unidentified mosses (sterile)										

any alga growing between tide-marks may be washed by fresh water during heavy rains at low tide.

The stand of any given alga may be pure over several square centimeters, a few decimeters, or, in some species, over some square meters. The vast majority of species, however, are mingled more or less abundantly with others, or occur sparsely, or even rarely as individuals, attached or free, often with no others of their kind within a distance of many meters. The latter is often true, *e. g.*, of *Agardhiella, Gracilaria, Porphyra,* etc. Where but one or a few collections of a species have been made, and all at one level, this level is given under "upper limit."

DIATOMACEÆ.

Besides the diatoms mentioned in Table G, a number of other species were identified by Dr. Albert Mann, in collections made on November 30, 1912, from the 3-foot level on two stakes in the middle of the harbor and from shells in the Inlet near the 1-foot level. They were not sought elsewhere and therefore their general distribution can not be given, as their colonies are not large enough to be conspicuous among the other algæ of their habitats. The following include all the diatoms thus far identified from the Inner Harbor:

Achnanthes brevipes Ag.
hauckii Grun.
longipes Ag.
Actinoptychus splendens (Shad.) Ralfs.
Amphora eulensteinii Grun.
Biddulphia aurita ,Lyngb.) Bred.
Cocconeis scutellum Ehrb.
Coscinodiscus asteromphalus Ehrb.
decrescens Grun.
excentricus Ehrb.
radiatus Ehrb.
Cyclotella striata (Kg.) Grun.
Fragillaria brevistriata Grun.
Fragillaria sp.
Gomphonema curvatum Kg.
Grammatophora marina Kg.
Licmophora tincta (Ag.) Grun.
Lithodesmium undulatum Ehrb.
Melosira borrei Grev.
nummuloides (Bory.) Ag.
Navicula alternans Schum.
grevillei (Ag.) Cleve.
kennedyi W. S.
lyra Ehr.
marina Ralfs.
smithii Breb.
Nitzschia acuminata W. S. Grun.
longissima (Breb.) Ralfs.
panduriformis (Greg.) Grun.
paradoxa (Gmel.) Grun.
sigma W. S.
Pleurosigma angulatum W. S.
balticum W. S.
distortum W. S.
intermedium W. S.
Podosira subtilis (Bail) Mann.
Synedra affinis.

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